Climate Change and Control of the Southeastern Bering Sea Pelagic Ecosystem

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ABSTRACT:

We propose a new hypothesis, the Oscillating Control Hypothesis (OCH), which predicts that pelagic ecosystem function in the eastern Bering Sea will alternate between primarily bottom-up control in cold regimes and primarily top-down control in warm regimes. The timing of spring primary production is determined predominately by the timing of ice retreat. Late ice retreat (late March or later) leads to an early, ice-associated bloom in cold water (e.g., 1995,1997, 1999), whereas no ice, or early ice retreat before mid-March, leads to an open water bloom in May or June in warm water (e.g., 1996, 1998, 2000). Zooplankton populations are not closely coupled to the spring bloom, but are sensitive to water temperature. In years when the spring bloom occurs in cold water, low temperatures limit the production of zooplankton, the survival of larval/juvenile fish, and their recruitment into the populations of species of large piscivorous fish, such as walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*) and arrowtooth flounder (*Atheresthes stomias*). When continued over decadal scales, this will lead to bottom-up limitation and a decreased biomass of piscivorous fish. Alternatively, in periods when the bloom occurs in warm water, zooplankton populations should grow rapidly providing plentiful prey for larval and juvenile fish. Abundant zooplankton will support strong recruitment of fish and will lead to abundant predatory fish that control forage fish, including, in the case of pollock, their own juveniles. Piscivorous marine birds and pinnipeds may achieve higher production of young and survival in cold regimes, when there is less competition from large piscivorous fish for cold-water forage fish such as capelin (*Mallotus villosus*). Piscivorous seabirds and pinnipeds may also be expected to have high productivity in periods of transition from cold regimes to warm regimes, when young of large predatory species of fish are numerous enough to provide forage. The OCH predicts that the ability of large predatory fish populations to sustain fishing pressure will vary between warm and cold regimes.

The OCH points to the importance of the timing of ice retreat and water temperatures during the spring bloom for the productivity of zooplankton, and the degree and direction of coupling between zooplankton and forage fish. Forage fish

(e.g., juvenile pollock, capelin, Pacific herring [*Clupea pallasii*]) are key for adult pollock and other apex predators. In the southeastern Bering Sea, important changes in the biota since the mid-1970s include a marked increase in the biomass of large piscivorous fish and a concurrent decline in the biomass of forage fish, including age-1 walleye pollock, particularly over the southern portion of the shelf. Populations of northern fur seals (*Callorhinus ursinus*), and seabirds such as kittiwakes (*Rissa* spp.) at the Pribilof Islands have declined, most probably in response to a diminished prey base. The available evidence suggests that these changes are unlikely the result of a decrease in total annual new primary production, though the possibility of reduced post-bloom production during summer remains. An ecosystem approach to management of the Bering Sea and its fisheries is of great importance if all of the ecosystem components valued by society are to thrive. Cognizance of how climate regimes may alter relationships within this ecosystem will facilitate reaching that goal.

1. Introduction

In the past 3 decades, major changes have occurred in the marine ecosystem of the southeastern Bering Sea (Vance et al., 1998; Hunt et al., 1999; Schumacher et al., In Press). Changes in the abundance of salmon, crab, and groundfish have caused significant economic impacts (NRC, 1996; Schumacher et al., In Press). Continuing declines in some populations of marine birds and pinnipeds have prompted protection measures such as trawling closures of critical feeding habitat of the endangered Steller sea lion (*Eumetopias jubatus*). This has disrupted fisheries and focused attention on the resilience of the ecosystem. Although harvests of marine species have undoubtedly affected the population dynamics of exploited species, there is a clear need for an understanding of the causal relationships between climate, primary and secondary production, and the population dynamics of upper trophic-level organisms (e.g., Livingston and Tjelmeland, 2000). This information is vital for understanding relative roles of climate variability and fishery harvests in structuring the Bering Sea ecosystem (Witherell et al., 2000).

In the early 1990s, hypotheses were developed to explain changes in the southeastern Bering Sea populations of top predators, such as the Steller sea lion and the red-legged kittiwake (*Rissa brevirostris*) (e.g., Anonymous, 1993). More recently, the focus broadened to explain changes in the structure of the marine ecosystem (e.g., NRC, 1996; Merrick, 1997). Several studies have identified the lack of forage fish (early life-stages of larger species or small fish species, in particular, those species with high lipid content) as being a factor in the declines of marine birds and pinnipeds (Sinclair, 1988; Anonymous, 1993; Sinclair et al., 1994, 1996; Decker et al., 1995; Hunt et al., 1996b; Merrick et al., 1997; Trites et al., 1999). Initially, these declines in forage fish abundance were hypothesized to result from predation by walleye pollock (*Theragra chalcogramma*) (Springer, 1992), and later from climate change (Piatt and Anderson, 1996; Springer, 1998, Anderson and Piatt, 1999).

Climate, and in a more immediate sense weather, determines sea ice cover, sea surface temperature, surface currents, and vertical mixing. Indices of winter

atmospheric and oceanic conditions, in conjunction with other parameters of ecosystems, have been used to identify shifts in climatic forcing and ecosystem response at decadal time scales (e.g., Trenberth and Hurrell, 1995; Mantua et al., 1997; Francis et al., 1998; Springer, 1998; Hare and Mantua, 2000; McFarlane et al., 2000; Hollowed et al., In Press). Two of these so-called "regime shifts" have been identified in the past thirty years. One occurred in the winter of 1976-1977, in which the Pacific Decadal Oscillation (PDO) underwent a strong transition and the Arctic Oscillation (AO) underwent a moderate transition; the second shift occurred in the winter of 1988-1989 when the PDO switched to a more-or-less neutral state, and the AO underwent a strong, persistent change (Ebbesmeyer et al., 1991; Hare and Francis, 1995; Sugimoto and Tadokoro, 1998; Beamish et al., 1999; Brodeur et al., 1999a; Hare and Mantua, 2000). Both the AO and the PDO are related to variability in the climate of the southeastern Bering Sea (Overland et al., 1999).

Identification of regime shifts depends not only on physical indices, but also on the responses of biological components of the ecosystem (e.g. Hare and Mantua, 2000). However, correlations between an atmospheric index and changes in fish, seabird or marine mammal populations leave unidentified the mechanisms by which climate and weather force biological processes. Additionally, the responses of upper-trophic-level organisms may lag changes in the physical system, as time is needed for energy flow and growth. It is necessary to understand the mechanisms by which climate and weather affect biological processes if we are to predict ecosystem responses to climate change.

Changes in the species composition and functional linkages of marine ecosystems can be influenced by both natural and anthropogenic factors. Natural factors in the Bering Sea include storm activity, sea-ice cover, ocean temperature and shifts in the location or strength of current systems. Direct anthropogenic factors include pollutants, removals of mammals and fish by hunting and fishing, and habitat disturbance. Both natural and anthropogenic factors can act as bottom-up regulators by modulating the amount of primary production, and thereby the abundance of prey

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available to higher trophic levels. Natural and anthropogenic factors can also exert top-down regulation by altering the abundance or distribution of predators available to crop prey. By removing vast quantities of whales, pinnipeds, fish and shellfish from the southeastern Bering Sea, large-scale commercial whaling and fishing exerted a top down effect on the marine ecosystem and changed the relative abundance of species, possibly opening the way for a single species, the walleye pollock, to dominate the pelagic biomass (Sinclair, 1988, Sinclair et al., 1994, 1996; NRC, 1996; Merrick, 1995, 1997).

In this paper, we evaluate two hypotheses. One is that a decline in annual new primary production caused declines in seabirds and pinnipeds. Alternatively, we hypothesize that changes in the marine climate may have caused primary production to go through different pathways or to different end points, thus diminishing its availability to seabirds and pinnipeds. Since juvenile walleye pollock are an important prey for birds and pinnipeds, and adult pollock are a potential competitor for forage fish, the control of pollock recruitment is central to these issues. Thus, we examine time series of physical and biological data from the eastern Bering Sea shelf for evidence of the effects of climate or weather on bottom-up and top-down regulation of the pelagic ecosystem. In particular, we investigate the role of the timing of ice retreat in determining the timing and fate of primary production and its effects on the recruitment of pollock and other large piscivorous fish. We suggest a new hypothesis, the Oscillating Control Hypothesis (OCH), that relates changes in fish, seabirds and marine mammals to decadal-scale climate variability.

2. STUDY AREA

The southeastern Bering Sea shelf is broad (> 500 km wide) and shallow (Fig. 1). During summer, shelf waters are differentiated into three domains (coastal, middle and outer) by hydrographic structure and currents associated with characteristic bottom depth ranges (Kinder and Schumacher, 1981; Coachman, 1986; Schumacher and

Stabeno, 1998; Stabeno et al., 2001). The coastal domain (depth < 50 m) typically is weakly stratified or well mixed as a result of tidal and wind mixing (Unimak, Peninsula and Inshore strata, Fig 1). In the middle shelf domain (depth 50 to 100 m), summer mixing energy is not sufficient to stir the entire water column in the presence of surface heat (South Middle Shelf and North Middle Shelf strata, Fig.1). As a result, a strongly stratified two-layered water column exists, with a wind-mixed surface layer (15 to 40 m), and a tidally mixed lower layer (> 40 m). During late July, the temperature difference between the upper and lower layers can be greater than 8° C; during summer, changes in density are dominated by temperature rather than salinity. The outer shelf domain (depth 100 to 200 m) has a wind-mixed surface layer and a tidally mixed bottom layer separated by a transition layer (South Outer Shelf and North Outer Shelf strata, Fig.1).

Three fronts or transition zones separate the domains. The middle transition and shelf-break front separate the middle shelf from the outer shelf, and outer shelf from the slope waters, respectively (Coachman, 1986; Schumacher and Stabeno, 1998; Stabeno et al., 1999). The inner or structural front, 5 to 30 km wide, separates the middle and coastal domains (Schumacher et al., 1979; Kachel et al., This Volume). This feature is evident along the entire southeastern shelf and continues northward west of Nunivak Island. A similar feature exists at the 50 m isobaths around the Pribilof Islands (Kinder et al., 1983). The inner front limits the horizontal flux of salt, nutrients and heat between the middle and coastal domains (Coachman, 1986; Kachel et al., This Volume). Increased production associated with the structural fronts at the Pribilof Islands enhances feeding opportunities for higher trophic level organisms (Sinclair et al., 1994; Decker and Hunt 1996, Hunt et al., 1996a, Brodeur et al., 2000).

Sea-ice and wind-forced mixing are important determinants of the timing and duration of spring primary production, and influence production of prey for larval fish (Napp et al., 2000). Sea-ice is formed in polynyas in the lees of islands and coasts (Niebauer et al., 1999). This ice is blown south by prevailing winds and melts at its southern edge, cooling the seawater (Pease, 1980; Niebauer et al., 1999). The maximum southerly extent of sea-ice varies greatly from year to year and affects bottom

temperatures on the shelf (Stabeno et al., 2001). Wind not only moves ice in winter, but it also affects the amount of mixing available to stir nutrients from depth to surface waters. In the Bering Sea, winter winds are strong, whereas summer winds, except for the occasional storm, are light. The summer storms are important, however, because of the new production that follows mixing events (Sambrotto et al., 1986).

High rates of primary production have been reported throughout the Bering Sea, especially on the northern shelf and along the edge of the eastern shelf (225 g C m^{-2} y^{-1}; Springer et al., 1996a). Over the southeastern Bering Sea shelf, primary production varies among domains, with the greatest production occurring in the outer (145 g C m^{-2} y^{-1}) and middle domains (135 g C m^{-2} y^{-1}; Springer et al., 1996a). Abundant nutrients and incident radiation support high primary productivity rates during the spring bloom. However, nutrients in the upper mixed layer become limiting within a short period over most of the shelf because of the establishment of a strong pycnocline (Whitledge et al., 1986). In the middle shelf domain, a chlorophyll maximum can persist in the pycnocline into the fall (Iverson et al., 1979a; Stockwell et al., 2001), implying that new production continues in this subsurface layer, as on other continental shelves (Holligan et al., 1984; Richardson and Christofferson, 1991). Mixing events from summer storms provide the only nutrient enrichment of surface waters on the middle and outer shelf (Whitledge et al., 1986; Sambrotto et al., 1986). In contrast, the frontal regions (outer, middle and inner) contain relatively large surface concentrations of both nutrients and phytoplankton throughout late spring and summer (Iverson et al., 1979a,b; Sambrotto et al., 1986; Kachel et al., This Volume).

3. Evidence for Change and Mechanisms

3.1 Climate, Physical Properties and Primary Production
3.1.1 Evidence for change in Climate and Physical Properties

To examine the effects of sea ice on spring primary production in the eastern Bering Sea, we obtained the position of the ice edge from 1972-1994 from the National Ice Center, the U.S. Navy's Fleet Numerical Meteorology and Oceanography Detachment and the National Climatic Data Center. For the years since 1994, we used the Alaska Regional Ice Charts, obtained as maps from the Anchorage Forecast Office of the National Weather Service. These maps were digitized, and the concentration of sea ice in each 1° block was obtained by averaging the concentration in each grid cell on a weekly basis.

Strong interannual variability in ice concentrations makes the statistical determination of decadal-scale variability difficult in this short time series (Fig. 2). Nevertheless, it is evident that interannual and decadal-scale variability in sea-ice coverage was greater at the southernmost edge of the ice field than farther north (Fig. 2). Between 57° and 58° N, there was an apparent decrease in days with ice after 1 January between 1972 - 1976 (mean number of days with ice 130 ± 18 SD) as compared with 1977 - 1989 (67 ± 26 SD, $t = 1.767$, $p = 0.096$) and 1990 - 2000 (76 ± 23.3 SD, $t = 2.036$, $p = 0.061$). The average pattern of ice coverage has also changed since the 1970s (Fig. 3), when the maximum extent of the zone in which 10% ice cover was present annually for > 2 weeks extended farther south and west than it did in the 1980s or the 1990s (Stabeno et al., 2001). Additionally, in the 1980s and 1990s, the zone where ice lasted for at least 2 weeks withdrew northeast along the Alaska Peninsula. Most of the north side of the Peninsula has been ice-free since 1990. The 1989 regime shift did not result in a return to the extensive ice conditions present before 1977.

The wind field has also changed dramatically over the past decades (Fig. 4). From the 1960s through the mid-1970s, strong winds were recorded at St. Paul Is. from late September through late April. Winter storms are now mostly over by April, as opposed to extending into May or even June, as was previously the case. Since about 1977, the period of summer calm has increased from about 3 months to 4 months, with calm winds predominating from June into October. Winds below the long-term (1965 to 2000) mean (611 m s^{-1} or 12 knots) have dominated the summer months of June, July and August since the early 1980s. In winter, winds are still sufficiently strong to result in a well-mixed water column and a vertical redistribution of nutrients. However, the tendency for decreased winds in summer has reduced the likelihood of summer mixing events.

The temperature of the water column in spring is crucial to the physiology of zooplankton and fish because warmer temperatures increase the rates of metabolic processes. Lacking a sufficiently long time series for integrated water column temperatures, we assessed long-term variation in spring and early summer sea surface temperatures (SST). We used the Global Ice and SST data set (Parker et al., 1993) and extracted a time series for 56° N, 165° W, a location representative of the middle-shelf domain. To document how the spring and summer warming of SST has changed since the 1960s, we plotted three-year running means of SST at monthly intervals from mid-April through mid-July (Fig. 5). There was a period of unusually low April and May temperatures in the early to mid-1970s. June and July SSTs also included a cold dip in the early 1970s. Over the period of record, warming has led to ~1° C increase in summer SST (e.g., the mid-July time series in Fig. 5). The linear fit to the 15 July time series has a slope of approximately 0.4° C/decade and this slope is positive at a confidence level > 95%. Since the water column is generally well mixed in early spring, spring SSTs also reflect temperatures lower in the water column. The diverging trend between spring and summer SSTs (spring SSTs are stable and are a proxy for temperatures below the pycnocline in summer, as warming at depth is minimal; summer SSTs are rising) suggests an increase in temperature stratification, but time-series of thermocline depth and strength are not available. The SST warming trend in June and

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July can be attributed to a combination of enhanced solar heating due to reduced cloud cover, and diminished evaporative cooling due to weaker winds (Fig. 5; Bond and Adams, This Volume). As emphasized by Bond and Adams (This Volume), the 40-year record for the Bering Sea suggests more of a long-term warming trend in the summer than in the winter climate.

3.1.2 Effects of Physical Change on Primary Production

Has the Amount of primary production changed?

If primary production is insufficient to meet the demands of herbivores, there will also be an impact on higher-trophic-level species, including marine birds and mammals. Thus, it is important to examine whether there is evidence for a decrease in new primary production that could account for declines in the populations of marine bird and mammals documented below. Unfortunately, there is no adequate time series of annual, spring or summer new primary production available to examine whether there has been either a secular or decadal-scale change in the amount of primary production over the eastern Bering Sea shelf. Thus, we have had to extrapolate probable long-term patterns of production from other data.

The amount of nitrate on the shelf sets a limit for new production from new nitrogen, as opposed to regenerated nitrogen (Dugdale and Goering, 1967), and a change in nitrate concentration or uptake could be an indication that primary production levels have changed. Pre-bloom nitrate concentrations in the middle domain in the 1990s were similar to those of the late 1970s (Whitledge, 1999; Rho et al., This Volume). Time series of salinity, which is correlated with pre-bloom nutrient levels, also suggest no long-term changes in the amount of nutrients available to support the spring bloom (Stabeno et al., This Volume). Profiles of nitrate concentrations over the middle shelf in May and June 1999 (Alpha Helix Cruise reports HX-209, HX-220; Rho et al., This Volume) had values of 10 - 15 µm nitrate, similar to those found in May and June of 1979 and 1981 (Whitledge et al., 1986). Recently, McRoy et al. (2001) calculated the average annual new production from the depletion of nitrogen in combination with an estimated diffusive re-supply. They found that over the 22 year period from 1979 to

2000 there was no evidence for a declining trend in new production. In fact, in 1997 and 1998, total new production was greater than that observed in the late 1970s and early 1980s (Rho et al., This Volume). Thus, the above studies suggest that there has been no decadal-scale decline in new spring primary production over the period from the 1970s to 2000, though the possibility of an increase cannot be ruled out.

In contrast, using the ratios of stable isotopes of carbon sequestered in the baleen of bowhead whales (*Balaena mysticetus*), Schell (2000) has argued that there has been a trend toward decreased rates of primary production since the mid-1970s. The interpretation of primary production rates from stable isotope ratios of carbon may be more complicated than previously recognized (Tortell et al., 2000; Gervais and Riebesell, 2001), and increases in water temperature or changes in the species composition of the phytoplankton may have influenced the change in ^{13}C that Schell observed (Libes, 1992).

If the zooplankton consumed by the whales in Schell's study were dependent on summer or fall production, the shift in ^{13}C observed by Schell could reflect a decrease in post-bloom production rates rather than a decrease in total annual production. Post-bloom storms in spring and summer result in a mixing of nutrients from below the pycnocline into the upper mixed layer, thereby supporting bursts of new production (e.g., Fig. 6, 1997, 1998) (Sambrotto et al., 1986; Whitledge et al., 1986). Calmer (Fig. 4), sunnier summers with a warmer upper mixed layer (Fig. 5; 1997 was an extreme example) decrease the likelihood of injection of nutrients into the upper mixed layer by storms (Sambrotto et al., 1986), and result in reduced summer contribution to annual new production. A decrease in summer primary production could affect the availability of food to support late-season copepod growth and thus availability of food for small fish, thereby compromising their over-winter survival.

Climate Change and the Timing of Production

In the southeastern Bering Sea, the timing of spring primary production is determined by a combination of the date of ice retreat, and stabilization of the water

column by solar heating and the cessation of strong storm activity (Sambrotto et al., 1986; Stabeno et al., 1998, 2001; Eslinger and Iverson, 2001). The timing of the spring bloom is important because it determines the ambient water temperatures in which grazers of the bloom must forage. Data illustrative of the conditions that determine the timing of the spring bloom were obtained from Mooring 2, located in ~ 72 m of water in the middle domain (Fig. 1, 6).

In the southeastern Bering Sea, there is sufficient light to support production as of mid-March, as evidenced by the presence of rapidly increasing amounts of chlorophyll beneath the ice in March 1995, 1997, and 1999 (Fig. 6). However, if ice retreat comes before mid-March, there is insufficient light to support net production in the well-mixed water column (e.g., Fig. 6, 1996, 1998, 2000). Without ice remaining after mid-March, the spring bloom is delayed until May or June, after winter winds have ceased and thermal stratification stabilizes the water column (Fig. 6) (Stabeno et al., 1998, 2001; Eslinger and Iverson, 2001). When spring winds are sufficiently strong to mix below the weak thermocline of April/May, the result is prolonged, moderate accumulation of phytoplankton, as occurred in 1996 and 1999 (Fig. 6). If ice melt occurs in April or May, there is an early, ice-associated bloom (e.g., Fig. 6, 1995, 1997, 1999). The pattern of late ice retreats with early ice-related blooms and early ice retreats with late blooms has held since the 1970s (Fig. 7). Although wind mixing of the water plays a role in determining when the bloom will occur, it is apparent in Fig. 7 that the timing of the last winter storm is less important than the date of ice retreat in determining the timing of the bloom. Thus, early blooms occur in cold water and are related to ice-edge blooms, whereas late blooms occur in relatively warm water and are not related to the ice-edge (Fig. 6, 8).

3.2 Zooplankton Populations: Temperature and the Fate of Primary Production
3.2.1 Evidence for Change in Zooplankton Populations

Evidence for change in zooplankton populations varies according to the season when sampled, species and location. Early analyses of the zooplankton biomass time series from the Hokkaido University summer cruises in the eastern Bering Sea

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suggested decreases from 1954 to 1995 in the wet weight of net zooplankton (excluding jellyfish) (Sugimoto and Tadokoro, 1997, 1998). However, most samples for this analysis came from the Bering Sea basin (water > 150 m deep) (Fig. 9) and may not have reflected conditions on the shelf. When data from these cruises were analyzed by domain with linear regression analyses on log transformed data, zooplankton biomass showed no statistically significant (p> 0.05) long-term trends over the shelf (Fig. 9), and no differences among time periods previously identified as having high, moderate or low biomass (Napp et al., This Volume). In contrast, by-catches of large jellyfish in the National Marine Fisheries Service (NMFS) bottom trawl surveys have increased over the shelf, particularly since 1990 (Fig. 10) (Brodeur et al., 1999a, In Press). Increases in jellyfish biomass commenced in the southern portion of the shelf prior to 1990 and subsequently spread northwestward after 1990. The increase in jellyfish represents a shift in energy flow that contributes little to the support of more economically valuable species.

Smith and Vidal (1986) compared spring zooplankton abundances in two years, one of which was somewhat cooler (1980, upper mixed layer 2.2 °C) than the other (1981, UML 5.1 °C). Over the middle shelf, spring abundances of *Pseudocalanus* and *Calanus* were higher in the warmer year. *Calanus marshallae*, a neritic copepod, produced two generations in 1981, but only one in 1980. More recently, Stockwell et al. (2001) and Napp et al. (This Volume) showed that the April-June biomass of neritic copepods (*Calanus marshallae*, *Pseudocalanus* spp., *Acartia* spp.) was significantly greater in the warm springs of 1997 and 1998 (integrated water column temperature 5.53 and 3.79 °C, respectively) than that in May and June of 1980 and 1981. Although there is evidence that these increases began as early as 1995 (Napp et al., This Volume), the incompleteness of the time series precludes determination of when these changes first occurred. In contrast to copepods, there was no statistically significant change in the biomass of adult and juvenile euphausiids (*Thysanoessa raschii*) over the shelf between samples taken in 1980/81 and those taken in 1997/98 (Stockwell et al., 2001; Coyle and Pinchuk, This Volume).

The differences between the results of Stockwell et al. (2001), Napp et al. (This Volume), and Coyle and Pinchuk (This volume) and the Hokkaido time series is likely a result of a difference in the seasons in which samples were obtained. The Hokkaido University summer cruises occurred in July and August, whereas Stockwell et al. (2001) and Coyle and Pinchuk (This Volume) sampled in May and June, and Napp et al. (This Volume) sampled in April and May. Comparisons could also be compromised by spatial or temporal aliasing if there are higher frequency fluctuations in the zooplankton that cannot be resolved by the sampling. Nevertheless, with the exception of 1995, the limited data available support the contention that the spring populations of neritic species of copepods have been greater in years when the spring bloom occurs in warmer water.

3.2.2 Mechanisms for Change in Zooplankton Populations

Zooplankton populations are regulated by both productivity and predation. The relative importance of bottom-up food limitation and top-down grazing by predators in controlling zooplankton biomass is a key element in understanding the control of energy flow in the eastern Bering Sea ecosystem.

Bottom-up Mechanisms:

Zooplankton production can be affected either by the availability or abundance of prey (phytoplankton and micro-zooplankton), or by the ability of the zooplankton to assimilate food and convert it into biomass or eggs. In the southeastern Bering Sea, the available evidence suggests that phytoplankton production during the spring bloom does not limit meso-zooplankton grazing rates. Dagg et al. (1982) estimated that meso-zooplankton grazing in 1979 accounted for only 18% of daily phytoplankton production in the outer shelf and 25% in the middle shelf domain, and that temperature, rather than food availability, limited copepod growth rates by its effects on zooplankton metabolic processes. Cooney and Coyle (1982), also working in 1979, estimated that copepods consumed 20% to 30% of primary production in the outer domain, and rarely > 5% of primary production in the middle domain.

The estimates of meso-zooplankton grazing rates by Dagg et al. (1982) and Cooney and Coyle (1982) were conducted in a year of unusually high abundance of age-1 pollock. Predation by juvenile pollock in that year may have limited the impact of copepod grazing more severely than usual. During a 15-year study of the eastern Bering Sea, including the shelf, between 1956 and 1970, Ikeda and Motoda (1978, in Cooney and Coyle, 1982) obtained grazing rates approximately 30% higher than those of Cooney and Coyle, indicating that copepod populations may have been more closely coupled to phytoplankton than in 1979. It is possible that we have underestimated zooplankton grazing rates, but the presence of a strong annual spring bloom suggests that, at least during the bloom, copepods are not limited by food availability.

Walsh and McRoy (1986) interpreted the presence of a sub-surface chlorophyll maximum in the middle domain as evidence of transfer of phytoplankton to the benthos, and a lack of tight coupling between primary production and copepod grazing. They hypothesized that the fate of production in the southeastern Bering Sea is influenced by water temperature, since phytoplankton growth is less sensitive to water temperature than is zooplankton growth (see also Vidal, 1980; Vidal and Smith, 1986; Townsend et al., 1994). Water temperature exerts a strong influence on the growth rates of zooplankton, and is often thought of as more important than food availability for limiting the growth rates of small-bodied copepods (McLaren, 1963; Corkett and McLaren, 1978; Vidal, 1980; Dagg et al., 1984; Huntley and Lopez, 1992). Thus, in years with warm water, Walsh and McRoy hypothesized that zooplankton would capture more of the primary production than in cold years, and the greater production of zooplankton in warm years would support the pelagic community, e.g., fish such as pollock. This scenario is similar to that in the Barents Sea, where zooplankton are able to crop more of the primary production in years when water temperatures are relatively high (Loeng, 1989). Thus, where interannual (and longer-term) variability in temperature is great, it is likely to play a major role in variation in copepod production (Smith and Vidal, 1984, 1986; Napp et al., 2000).

Coupling between meso-zooplankton and phytoplankton stocks is likely to be particularly weak in years when ice-associated spring blooms dominate the annual total primary production. When water temperatures during the spring bloom are cold (< 2^0 C), as occurs when there is an ice-edge bloom, zooplankton reproduction and population growth will be retarded and the spring phytoplankton bloom will be less vulnerable to control by zooplankton grazing (Napp et al., 2000). Therefore much of the phytoplankton production will sink ungrazed to the bottom to support a rich benthic food web (e.g., clams, crabs and flatfish; Livingston et al., 1999). In contrast, during spring blooms when water temperatures are relatively warm (> 4 ^{o} C), as is the case when an open-water spring bloom occurs in May or June, meso- and microzooplankton reproduction and population growth will occur at higher rates. For example, Coyle et al. (1996), in assessing Russian studies of zooplankton on the shelf, note that concentrations of *C. marshallae* and *Pseudocalanus* spp. on the middle shelf were denser in warmer years.

Top-down Mechanisms:

Consumption of zooplankton by fish can also limit zooplankton population growth and biomass, although there is no direct evidence to evaluate the role of predation in determining the biomass of copepods in the eastern Bering Sea. The results of modeling indicate that between 80% (Trites et al., 1999; Kerim Aydin, Pers. Comm.) and 100% (Springer, 1992) of copepod production in the outer and middle domains is consumed. The majority of predation on copepods is caused by larger plankton such as euphausiids and gelatinous zooplankton, with a smaller but substantial portion of mortality being caused by juvenile and adult pollock (Kerim Y. Aydin, Pers. Comm.). In recent years (1994-1999), an inverse relationship between zooplankton biomass and age-0 pollock abundance has been observed at the end of summer around the Pribilof Islands and suggests that pollock are capable of depressing prey stocks (Swartzman et al., ms). Similarly, Sugimoto and Tadokoro (1997) have shown that there is a biennial fluctuation of zooplankton biomass in the Bering Sea basin that is negatively correlated with the catch of Asian pink salmon (*Oncorhynchus gorbuscha*).

Two sources of predation on zooplankton increased between the 1970s and the 1990s. First, large scyphomedusa jellyfish, which eat zooplankton as well as small fish, have increased exponentially since the late-1980s (Fig. 10) (Brodeur et al., 1999a, ms). One jellyfish species, *Chrysaora melanaster*, was estimated to consume about one-third of the zooplankton standing stock around the Pribilof Islands in summer 1999, compared to a consumption of < 1% in 1982 (Brodeur et al., In Press). Second, the numbers of baleen whales, such as humpback (*Megaptera novaengliae*) and minke (*Balaenoptera acutorostrata*) whales have also increased over the shelf since the 1970s (Baretta and Hunt, 1996). The diet composition of these whales in the eastern Bering Sea is not known, and their impact on zooplankton has yet to be determined.

3.3 Changes in Fish Populations

3.3.1 Evidence for Change in Fish Populations

We used the results of the NMFS bottom trawl surveys to examine changes in fish populations over the eastern Bering Sea shelf. These trawls have been conducted with similar methods, over the same region and at the same time of year since 1982 (Bakkala, 1993). Surveys in 1976 and 1979 differed slightly from surveys in 1982 and after, but were sufficiently similar to provide useful comparisons with the post-1982 surveys. The bottom trawl survey stations are at the centers of a 20 nautical mile grid (in the vicinity of the Pribilof Islands the corners of the grid are also sampled with a distance of 14.4 nautical miles between stations), and have a goal of sampling 356 trawl stations each summer. The Unimak Stratum (Fig. 1) has the lowest number of stations (8). The surveys sample demersal and semi-demersal populations well, and provide an index of mid-water organisms such as age-2 and age-3 pollock and some forage fish which are caught as the net travels to and from the bottom (Brodeur et al., 1999b). This survey provides the longest quantitative time series available for examining trends in fish populations of the eastern Bering Sea. Data are reported in Catch Per Unit Effort (CPUE) (kg/ha), which is a proxy for normalized biomass.

Adult Fish

Across the shelf, populations of two gadids (e.g., pollock, and Pacific cod, *Gadus macrocephalus*) and flatfish (e.g., arrowtooth flounder, *Atheresthes stomias*, northern rock sole, *Lepidopsetta polyxystra*) increased in the late 1970s to early 1980s and then stabilized through the rest of the 1980s (Fig. 11). Of particular importance to these biomass trends was the maturation of the immense 1978 year-class of pollock. Concurrent with increases of adult gadids and piscivorous flatfish were decreases in forage fish such as capelin (*Mallotus villosus*), herring (*Clupea pallasi*), eulachon (*Thaleichthys pacificus)* and age-1 pollock (Fig. 11, best seen in the 3-year running mean). The biomass of both gadids and flatfish in 1999 was more than three times that present in 1975, and would require a large biomass of forage fish to support their metabolism and growth.

Adult walleye pollock make up the bulk of the gadids present on the shelf. The distribution pattern of age-2 and older pollock (age-2+) has changed since 1975, when the highest densities of pollock biomass were in the South Outer Shelf (42% of pollock biomass) and South Middle Shelf (22% of pollock biomass) strata (Fig. 12). By the late 1990s, densities had declined over most of the southern portions of the shelf. The biomass of age-2+ pollock apparently remained high in the North Outer Shelf and North Middle Shelf strata. These changes resulted in a major northward shift in the distribution of pollock biomass, with 81% of the biomass in the North Outer Shelf and North Middle Shelf strata in 1999 as compared to only 31% in 1975. The abrupt declines in pollock biomass in many of the strata since 1996 and the overall decline in pollock biomass between 1995 and 1999 may indicate that pollock have shifted their distribution northward, outside of the survey area. Alternatively, populations may have declined, possibly because of the decrease in forage fish on which adult pollock and other predatory fish depend.

Arrowtooth flounder are important higher-trophic level predators of forage fish including juvenile pollock. Examination of their biomass by strata (Fig. 13) on the shelf showed that they were initially most abundant in the South Outer shelf and Unimak

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strata (5-10 kg/ha), and then increased after 1980 except in the Inshore stratum. Biomass maxima were measured for most strata between 1992 and 1996, and, with the possible exception of the Southern Outer Shelf and Unimak strata, showed strong declines in biomass subsequent to 1997. This species has also greatly increased in the Gulf of Alaska (STOCK ASSESSMENT DOCUMENTS).

Juvenile and Forage Fish

The biomass of forage fish is dominated by age-1 pollock and herring. Forage fish populations show great interannual variation (Fig. 11), some of which is accounted for by variation in the abundance of age-1 pollock (Fig. 12). In virtually every stratum, the estimated biomass of age-1 pollock was highest in either 1975 or 1979, and at or near its lowest in 1998-1999 (Fig. 12). In all strata, as age-2+ pollock increased in biomass between 1975 and 1984, age-1 pollock decreased, possibly because of cannibalism. Despite several strong year classes since the very strong 1978 year-class, the biomass of age-1 pollock has remained low except in the North Outer Shelf stratum. Age-1 pollock have fallen to particularly low levels across the southern shelf.

Capelin is a fat-rich forage fish species that is important in the diets of marine birds and mammals (Hunt et al., 1996b; Piatt and Anderson, 1996; van Pelt et al., 1997). In summer, capelin move inshore to spawn along the western Alaska coast, while non-spawners inhabit the seaward part of the shelf (Pahlke, 1985). Although formerly available to marine birds and pinnipeds breeding on the Pribilof Islands, the summer biomass of capelin around the Pribilof Islands declined in the mid- to late-1970s (Hunt et al., 1996b; Naumenko, 1996). In the late 1980s, capelin had moved well north of the Pribilof Islands (Brodeur et al. 1999b).

Capelin prefer cold water within a narrow temperature range (< 2.0º C) (Methven and Piatt, 1991; Naumenko, 1996). In the Barents Sea, they move large distances to stay in water with temperatures between $-1°$ and $+ 2°$ C (Loeng, 1989), and in the Bering Sea avoid near-bottom water temperatures above 2.0º C (Naumenko, 1996). In 1976, the bottom temperature near the Pribilof Islands was about 0° C, whereas in

1977, the temperature was 3° C (Overland et al., 1999). Trawl surveys by the NMFS
obtained a plentiful by-catch of capelin near the Pribilof Islands in summer 1975, but not
in 1978 or years thereafter (Hunt et al., 1996b), when capelin were distributed to the
north in cooler waters (Brodeur et al., 1999b). The failure of capelin to return to the
vicinity of the Pribilof Is. in the early 1980s, when bottom temperatures were sufficiently
cool (2° C), may reflect competition or predation pressure from pollock, but there is no
evidence available to support this conjecture.

3.3.2 Mechanisms for change in fish populations

Warming sea temperatures and changes in bottom temperatures over the shelf
during the past decades could have played a significant role in the changes in fish
distributions recorded here. The northern shelf is highly productive (225 g C m^{-2}y^{-1},
Springer et al., 1996a). Increasing water temperatures and decreasing ice cover may
have facilitated the northward spread of pollock, Pacific cod, rock sole and arrowtooth
flounder. Warmer temperatures also could have pushed capelin north from the vicinity
of the Pribilof Islands, where they were formerly abundant.

The horizontal and vertical distribution of pollock is temperature dependent
(Bailey et al., 1999). Age-1 pollock avoid water colder than 2º C (Wyllie-Echeverria,
1996). During years of warm water temperatures and reduced ice cover, the region of
cold bottom-waters (2 °C) on the shelf shrinks and age-1 pollock extend their range
northward (Wyllie-Echeverria, 1995). In winters with heavy ice cover in the eastern
Bering Sea, age-1 pollock are more constrained to the southwestern portion of the shelf
near the shelf edge.

Pollock in the eastern Bering Sea have stronger year-classes in warm years
(Wespestad, 1991 in Balykin, 1996; Bulatov, 1995; Quinn and Niebauer, 1995),
particularly when spawning stocks are small (Khen, 1987, in Balykin, 1996), and when
prevailing winds advect eggs and larvae away from cannibalistic adults (Wespestad et
al., 2000). Likewise, in the western Bering Sea, the year-class strength of Pacific cod is
inversely associated with ice cover during the spawning period in early April (Vinnikov,

1996). The development and growth of juvenile pollock is accelerated in warmer waters (Haynes and Ignell, 1983; Nakatani and Maeda, 1984; Bailey et al., 1995, 1996), perhaps in part because of greater abundance of zooplankton. Ice and cold temperatures significantly delay hatching of pollock eggs, which may result in higher total egg mortality (Blood, This Volume), and causes a mismatch between the peak abundance of larval pollock and their prey (Napp et al., 2000). Between 1964 and 1988, Quinn and Niebauer (1995) found a strong positive relationship between the survival of pollock to age two and temperature during and after the first winter (see also Ohtani and Azumaya, 1995).

The survival of young pollock may be influenced by vulnerability to predation. Older pollock are cannibalistic (Dwyer et al., 1987; Wespestad, 1994; Balykin, 1996, Wespestad and Quinn, 1996). On the southeastern Bering Sea shelf, cold bottom waters in winter may force age-1 pollock to the shelf edge where adult pollock are more abundant, thus exposing juveniles to cannibalism (Dwyer et al., 1987; Ohtani and Azuma, 1995; Wyllie-Echeverria, 1995). Since the mid-1980s in the Gulf of Alaska, pollock recruitment has been more strongly controlled by flatfish and cod predation on juveniles than it is by environmental effects on larvae (Bailey, 2000). Increases in cod and flatfish, in particular arrowtooth flounder, may also have a negative effect, via predation, on the survival of juvenile pollock in the Bering Sea, as do cannibalistic adult pollock (Livingston and Methot, 1998; Lang et al., 2000; Livingston and Jurado-Molina, 2000).

3.4 Changes in the Populations and Diets of Pinnipeds and Seabirds
Since the mid-1970s, there have been significant declines in the populations of pinnipeds at the Pribilof Islands (York and Kozloff, 1986; Loughlin et al., 1994; NMFS, Unpubl. Data). There, the population of Steller sea lions has almost disappeared (NMFS, Unpubl. Data), and the population of northern fur seals, the pinniped with the highest biomass in the Bering Sea, has decreased significantly (York and Hartley, 1981; York and Kozloff, 1986; NMFS, 1993, 1995). Counts of fur seal pups, indicative of the number of breeding females on the Pribilof Is. declined steeply between 1976 and the

mid-1980s (Fig. 14) (York et al., 2000), with the reduction on St. Paul Is. being about 33%, and on St. George Is. about 60%. The differences in rate and length of population declines on the two islands may reflect differences in the foraging habitats used by the two populations; fur seals on St Paul Is. tend to forage in the North Outer Shelf and North Middle Shelf strata, whereas those on St. George Is. tend to forage in the South Outer Shelf and South Middle Shelf strata (see Fig. 10 for differences in forage fish distributions by strata) (Antonelis et al., 1997; Robson, 2002). On the north side of the Alaska Peninsula, harbor seal (*Phoca vitulina*) numbers at haulouts have also decreased by about half (Fig. 15) (Withrow and Loughlin, 1995).

Since the mid-1970s, there has also been a significant decline in the numbers of seabirds, particularly kittiwakes (Fig 16) and thick-billed murres (*Uria lomvia*), breeding at the Pribilof Islands (Hunt and Byrd, 1999; Dragoo et al., 2000). Production of kittiwake and murre (*Uria* spp.) young at the Pribilofs declined between the 1970s and the early 1980s (Hatch, et al., 1993; Decker et al., 1995; Hunt et al., 1996b), possibly in response to competition with adult pollock for forage fish, including age-1 pollock (Livingston et al., 1999).

Changes in the diets of fur seals and seabirds at the Pribilof Islands reflect declines in the availability of key prey species. For example, diets of fur seals in the eastern Bering Sea changed dramatically between samples obtained between 1960 and 1974 and those from the 1980s and 1990s (Fig. 17). Fur seal diets sampled at sea between 1960 and 1974 were spread evenly over a number of taxa, capelin and squids (not shown in Fig. 17) were more important than adult pollock (age-2) (Kajimura, 1984; Fiscus, Pers. comm.), and herring and eulachon were important, but variable dietary components (Kajimura, 1984). Similarly for kittiwakes and murres breeding on the Pribilof Is. in the 1970s, capelin and the large pelagic amphipod, *Themisto libellula*, both cold-water species, were important dietary components (Decker et al., 1995; Hunt et al., 1996b,c).

By the early 1980s, samples of fur seal diets obtained at-sea were dominated by juvenile pollock (ages-0-1). Greenland turbot (*Reinhardtius hippoglossoides*), capelin and eulachon were no longer eaten (presumably because they were no longer available), and sand lance (*Ammodytes hexapterus*) had increased in importance (Fig. 17) (Sinclair, 1988; Sinclair et al., 1994, 1996). In 1987 and 1988, capelin were also no longer present in the diets of kittiwakes and murres at the Pribilof Is. (Hunt et al., 1996b), and the proportion of sand lance in seabird diets had increased. Similarly, in 1988 and 1990 fur seal diets on St. George and St Paul Is. were dominated by juvenile pollock, while capelin and Greenland turbot remained absent from the diets (Antonelis et al., 1997).

Changes in fur seal, kittiwake and murre diets at the Pribilof Is. have resulted in dependence on smaller prey and prey with a lower energy density. Pollock have consistently been an important component of seabird and fur seal diets at the Pribilof Islands. Between the 1970s and 1980s, there was a shift from the use of age-1 pollock by seabirds to the consumption of much smaller age-0 pollock (Hunt et al., 1996c), reflecting the decrease in age-1 in pollock near the Pribilof Is. (Fig 12). After the 1960-1974 collection, fur seal diets shifted from a predominance of adult pollock to the use of age-2 and younger pollock, which are less valuable because of the difference in size. Juvenile pollock are not a good substitute for capelin because capelin have a higher energy density (4.3 kJ/g wet weight) than juvenile pollock (2.7 kJ/g wet weight) (van Pelt et al., 1997). Although sand lance have about the same energy density as capelin, they are smaller and seabirds have higher reproductive success when provisioning chicks with capelin (Baird, 1990).

The declines in the populations of several species of marine birds and pinnipeds in the shelf waters of the southeastern Bering Sea imply that the carrying capacity of the region for these birds and pinnipeds has decreased. Shifts in their diets indicate that the decrease in carrying capacity involves not just a reduction in the amount of preferred prey available, but also a change in the structure of the food webs that support these top predators. The timing of these declines suggests that they and the

accompanying shifts in diet may have been related to the regime shift of 1976. The observations of population decreases and diet shifts among these top predators point to a need to understand how both bottom-up and top-down control might be influencing the availability of prey. Because pollock biomass dominates the ecosystem of the eastern Bering Sea shelf, and because pollock is both an important prey and a competitor for birds and pinnipeds, understanding the control of pollock recruitment is critical.

4. CONCEPTUAL MODELS

An early model of energy flow in the middle domain of the eastern Bering Sea ecosystem emphasized a dichotomy between energy going to the benthos in cold years and to the pelagic ecosystem in warm years (Walsh and McRoy, 1986). However, the simultaneous increase in both pelagic (pollock) and demersal (Pacific cod, arrowtooth flounder) fish over the shelf suggests that a greater flux of energy to zooplankton in warm years may benefit predators in both habitats, and recent simulations indicate that an increase in zooplankton should benefit all upper trophic level organisms, including marine birds and mammals (Trites et al., 1999). Thus, to understand the simultaneous increases in the biomass of some fish and declines in other fish, seabirds and pinnipeds, we need to look for mechanisms that would alter the pathways and recipients of energy flow in the marine ecosystem. The coincidence of many of the changes in fauna with shifts in climate regimes suggests that investigation of mechanisms that could tie changes in fish biomass to climate might be profitable (Napp and Hunt, 2001).

Based on available time series and process studies, several relationships appear to be important in governing production and its fate in the southeastern Bering Sea. In many cases, these proposed relationships need further testing.
1) The timing and duration of ice cover and winter winds determines the onset of spring net primary production.

2) The amount and timing of spring and summer storm activity, coupled with pycnocline strength, strongly influence the amount of annual new production.

3) Water temperature and grazing by forage fish and other planktivores control the biomass of crustacean zooplankton. All else being equal, years in which the spring bloom occurs in warm water, and/or years with prolonged spring production, should have higher meso-zooplankton production than years in which the bloom occurs in cold water at the ice edge. Warm-water blooms may also result in a larger biomass of zooplankton than cold-water years or years in which new production is confined to a brief, intense early pulse. The lack of tight coupling between zooplankton production and primary production makes difficult the detection of the responses of zooplankton (and fish recruitment) to variations in primary production (Runge, 1988).

4) Copepod production is fully or nearly fully consumed by planktivores (fish, euphausiids and gelatinous zooplankton).

5) In years when the biomass of adult pollock and other large predatory fish (e.g., Pacific cod, arrowtooth flounder) is high and spatial overlap of adult fish and juvenile pollock is large, predation by large piscivorous fish will strongly influence pollock year-class strength (e.g., Laevastu and Bax, 1991).

6) Other than the fisheries harvest, the availability of forage fish and other prey determine the biomass of adult pollock and that of other large predatory fish.

7) The composition and biomass of the forage fish assemblage together determine the recruitment success of pinnipeds and seabirds.

8) Effects of climate on food availability, rather than the direct effects of predation, control present-day populations of marine birds, whales and most likely fur seals in the Bering Sea.

The information assembled in this paper indicates that the effect of climate on ice cover and water temperature has a pervasive effect on the timing and fate of production (Figs. 6,7, 8), the distribution of forage fish and predatory fish (Figs. 10, 12, 13), and the availability of forage fish for predation by birds, mammals and large predatory fish (Fig. 17). Inverse relationships between the biomass of various combinations of predator

and prey species suggest changes between top-down and bottom-up control mechanisms that may be related to decadal-scale changes in climate or water temperature and that have yet to be addressed (Trites et al., 1999).

4.1 The Oscillating Control Hypothesis

The coupling between forage fish and zooplankton, and between forage fish and large predatory fish may be either top-down or bottom-up. Two factors control these relationships: (1) If large piscivorous fish are sufficiently abundant, control of forage fish abundance will be top-down, and forage fish production and biomass will be uncoupled from zooplankton production. In this case, zooplankton may be abundant and more strongly coupled to phytoplankton than when forage fish crop down zooplankton populations. (2) If populations of large piscivorous predatory fish are scarce, then larval fish and forage fish (including juvenile pollock) will be subject to less severe predation pressure. Recruitment of both predatory fish and forage fish will be determined during the larval stage, and the abundance of zooplankton will play an important part, i.e., control of forage fish abundance will be bottom-up. In this case, forage fish (including age-0 pollock) may depress meso-zooplankton standing stocks. Zooplankton may or may not be uncoupled from phytoplankton production, but their biomass will appear uncoupled because of zooplankton consumption by fish. Water temperature will affect the coupling of phytoplankton, micro-zooplankton and meso-zooplankton as well as the survival of fish eggs and larval production. However, only when large predatory fish are scarce and unable to exert significant predation pressure on forage fish will temperature have an effect on forage fish biomass by modulating food supply, i.e., zooplankton biomass. We also suggest that there may be abrupt shifts between predominately top-down and bottom-up control [see also Steele and Henderson (1984) and Spencer and Collie (1996) for models that predict rapid ecosystem change]. The following view of the Bering Sea builds on conceptual models proposed by Sætersdal and Loeng (1987), Loeng (1989), Beamish (1993), Bulatov (1995), and Bailey (2000) for other ocean regions.

We propose a new hypothesis, the Oscillating Control Hypothesis (OCH), which extends the model of Walsh and McRoy (1986). The OCH provides a conceptual framework for understanding how decadal-scale changes in ocean climate could affect the relative importance of bottom-up and top-down control of the trophic structure of the southeastern Bering Sea ecosystem.

The OCH predicts that during cold regimes (late ice retreat and cold water during the spring bloom), zooplankton prey for larval fish will be in short supply, fish egg-mortality will be higher, and strong year-classes for pollock and other fish should be infrequent. Under this regime, recruitment to many fish populations will be weak in most years because the system is primarily constrained by bottom-up processes (Fig. 18). Pinnipeds and piscivorous seabirds, however, may thrive if species of forage fish that prefer cold water, such as capelin, change their distribution and become available near rookeries and colonies.

In contrast during warm regimes (early ice retreat and warm water during the spring bloom), the OCH predicts that there should be consistently strong production of zooplankton and, based on high survival of larval and juvenile fish, the potential for large year classes of pollock and other piscivorous fish (Fig. 18). The increased frequency of large year classes since the switch to a warm regime in 1976/77 is consistent with this prediction (Hollowed et al., In Press). However, as the warm regime continues over time and several year classes have average to above average recruitment, the biomass of adult predatory fish (e.g. pollock, Pacific cod, and arrowtooth flounder) will increase, and control will switch to being primarily top-down (e.g., Bailey, 2000). When forage fish are strongly limited by top-down processes, there should be more zooplankton to support other planktivore populations (e.g., chaetognaths, jellyfish, salmon and baleen whales). Conversely, the reduction in forage fish abundance should cause declines in the populations and productivity of pinnipeds and piscivorous seabirds. By limiting the buildup of the biomass of pollock and other large piscivorous fish, fisheries harvests may ameliorate the top-down control of the predators but may further depress forage fish populations if bycatch is high.

The OCH differs from the hypothesis of Sugimoto and Tadokoro (1997) in that they propose that bottom-up controls work at the decadal-scale, whereas top-down controls work at a biennial or annual-scale. Because they believe that zooplankton is limited by primary production, they emphasize the importance of decadal-scale variation in wind mixing that would enhance primary production. However, we believe that there is insufficient evidence for food limitation of zooplankton production on the middle shelf, and argue alternatively that water temperature is a more important control of zooplankton production (as do Tomosada and Odate, 1995, as cited in Sugimoto and Tadokoro, 1997). Both water temperature and wind mixing may well be important. Rather than arguing for either top-down or bottom-up control, we suggest that both forcing mechanisms are likely to operate, but in significantly different proportions depending on climate regime (Roff et al., 1988; Reid et al., 2000).

The speed and effects of shifts between cold and warm regimes are likely to be asymmetrical. When there is a shift from a cold regime to a warm regime, zooplankton food will initially be plentiful for larval and juvenile fish, and predation from adults should be weak. Thus, there should be an almost immediate surge in forage fish (except cold water fish such as capelin) and pollock year-class strength due to high larval and juvenile survival (e.g., age-1 pollock in 1978 and up to 3 years following). In contrast, after a shift from a warm to a cold regime, it will take some time for the populations of adult predatory fish to decline sufficiently that top-down control relaxes. Thus, during the transition from a warm regime to a cold regime, recruitment will be affected by both top-down and bottom-up controls. During this transition, these fish will be particularly vulnerable to over-fishing as their rate of recruitment will be low.

The effects of interannual variations in water temperatures at the time of the spring bloom will differ depending on whether they occur in a cold or warm regime. A cold year in a warm regime will not change the system from top-down to bottom-up control because the large biomass of predatory adult fish will persist and continue to exert top-down control. In contrast, one or two warm years in a cold regime could lead

to a switch from bottom-up to top-down control if sufficiently large year classes of piscivorous predators, such as pollock, were produced.

Interannual variation in forage fish and pollock year-class strength can also be expected, particularly within warm regimes, because of the changing spatial distributions of adult predators and forage fish. As the populations of adults redistribute themselves seeking preferred water temperatures, there will occur areas where juvenile fish are temporarily free of predators. If adequate zooplankton resources are available in these refugia, larval and juvenile survival may be high. Wespestad et al. (2000) suggested a mechanism for inshore transport of larval and juvenile pollock, which could lead to segregation from cannibalistic adults, and the potential for strong year classes. Year class strength and simulated transport data appear to support their hypothesis.

The above hypotheses suggest a number of testable relationships:

1)   If zooplankton production is decoupled from primary production, then we should see interannual and interdecadal variation in zooplankton biomass tied to either water temperature or predator demand, but not to annual primary production rates. However, variability in the flux of phytoplankton to the benthos should be strongly correlated with spring primary production and summer winds. Since measurement of annual rates of primary production is difficult, comparison of variation in spring and summer sedimentation rates with zooplankton production and water temperature may be instructive. Testing these relationships will require development of a rigorous time series of zooplankton production over the shelf and monitoring with sediment traps.

2)   If forage fish grazing controls zooplankton biomass and the strength of coupling of zooplankton production to phytoplankton production, there should be an inverse relationship between the abundance of forage fish and the strength of coupling between zooplankton and phytoplankton. More information is required about the consumption of zooplankton by

larval fish (e.g., Dagg et al., 1984; Hillgruber et al., 1995; Napp et al., 1996, 2000), juvenile pollock (Ciannelli et al., 1998; Schabetsberger et al., 2000) and other forage fish under a variety of temperature and prey-density regimes.

3) In warm regimes, the biomass of adult pollock and other predatory fish will increase, and these predators will compete with other apex predators such as pinnipeds and marine birds for forage fish, with the result that bird and pinniped populations may decline. In cold regimes, once the biomass of adult pollock and other predatory fish have declined, forage fish may be more available to pinnipeds and marine birds.

4) In warm regimes, adult pollock should be able to sustain a relatively intense fishery, as compared to during a cold regime, as removals of cannibalistic adults should permit increased survival of juveniles and improved recruitment. In cold regimes, adults removed by the fishery will not be quickly replaced because the system is limited from the bottom up by the availability of zooplankton to juveniles. Thus the rate of change in biomass will be asymmetrical.

5) As suggested by Merrick (1995, 1997), the removal of large numbers of previously abundant planktivorous whales and fish may have released a large biomass of zooplankton for consumption by pollock. If the numbers of baleen whales increase, their grazing of zooplankton should impact the availability of zooplankton for other planktivores, including forage fish. If baleen whales consume large quantities of larval and juvenile forage fish, they will compete directly with apex predators such as seabirds, small cetaceans, and pinnipeds. We need more information about the distribution, biomass, prey consumption and dietary composition of large cetaceans if we are to evaluate their impact on the ecosystem. Diet and consumption data of other top predators, such as seabirds or pinnipeds, may provide useful insights into the impact of whales on the availability of zooplankton and juvenile fish.

If spring and summer water temperatures are key to the productivity of zooplankton, and the degree and direction of coupling between zooplankton and forage fish are key to the support of adult pollock and other apex predators, we need to refocus our energies on these parts of the food web. Knowledge of zooplankton coupling to juvenile pollock and other forage fish is critical, as is understanding the role of apex predators other than pollock in this ecosystem. An ecosystem approach to management of the Bering Sea is vital if all of the ecosystem components valued by society are to thrive. Cognizance of how natural climate regime fluctuations and anthropogenic climate change may alter relationships within this ecosystem will facilitate reaching that goal.

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References Cited

Alexander, V., Cooney, T., 1979. A quantitative study of the phytoplankton from the eastern Bering Sea. In: Environmental Assessment of the Alaska Continental Shelf. NOAA/OCSEAP, Annual Report.

Anderson, P.J., Piatt, J.F., 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology Progress Series 189, 117-123.

Anonymous, 1993. Is It Food? Addressing marine mammal and seabird declines. Workshop Summary. Alaska Sea Grant Report 93-01.

Antonelis, G.A., Sinclair, E.H., Ream, R.R., Robson, B.W., 1997. Inter-island variation in the diet of female northern fur seals (*Callorhinus ursinus*) in the Bering Sea. Journal Zoological Society London 242, 435-451.

Baduini, C.L., 2000. The Influence of Anomalous Weather and Ocean Conditions on the Foraging Ecology and Provisioning Patterns in Shearwaters. Ph.D. thesis, Univ. of California at Irvine, Irvine, California, USA, unpublished.

Baduini, C.L., Hyrenbach, K.D., Coyle, K.O., Pinchuk, A., Mendenhall, V., Hunt, G.L., Jr., 2001a. Mass mortality of short-tailed shearwaters in the southeastern Bering Sea during summer 1997. Fisheries Oceanography 10, 117-130.

Baduini, C.L., J.R. Lovvorn, and G.L. Hunt, Jr., 2001b. Determining the nutritional condition of short-tailed shearwaters (*Puffinus tenuirostris*): implications for migratory flight ranges and starvation events. Marine Ecology Progress Series, In Press.

Bailey, K.M., 2000. Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. Marine Ecology Progress Series 198, 215-224.

Bailey, K.M., Brown, A,L., Yoklavich, M.M., Mier, K.L., 1996. Interannual variability of growth of larval and juvenile walleye pollock in the western Gulf of Alaska. Fisheries Oceanography 5 (Supplement 1), 137-147.

Bailey, K.M., Canino, M.F., Napp, J.M., Spring, S.M., Brown, A.L., 1995. Contrasting years of prey levels, feeding condition and mortality of larval walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. Marine Ecology Progress Series 119, 11-13.

Bailey, K.M., Powers, D.M., Quattro, J.M., Villa, G., Nishimura, A., Traynor, J.J., Walters, G., 1999. Population ecology and structural dynamics of walleye pollock (*Theragra chalcogramma*). In: Loughlin, T.R., Ohtani, K. (Eds.), Dynamics of the Bering Sea: A Summary of Physical, Chemical, and Biological Characteristics, and a Synopsis of Research on the Bering Sea. North Pacific Marine Science Organization (PICES), University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, Alaska, USA, pp. 581-614.

Baird, P.A., 1990. Influence of abiotic factors and prey distribution on diet and reproductive success of three seabird species in Alaska. Ornis Scandinavica 21, 224-235.

Bakkala, R.G., 1993. Structure and historical changes in the groundfish complex of the eastern Bering Sea. NOAA Technical Report NMFS 114, 91pp.

Balykin, P.A., 1996. Dynamics and abundance of western Bering Sea walleye pollock. In: Mathisen, O.A., Coyle, K.O. (Eds.), Ecology of the Bering Sea: A review of Russian literature. Univ. Alaska Sea Grant Report 96-01, Fairbanks, Alaska, pp. 177-182

Baretta, L., Hunt, G.L., Jr., 1994. Changes in the numbers of cetaceans near the Pribilof Islands, Bering Sea, between 1975-78 and 1987-89. Arctic 47, 321-326.

Beamish, R.J., 1993. Climate and exceptional fish production off the west coast of North America. Canadian Journal of Fisheries and Aquatic Science 50, 2270-2291.

Beamish, R.J., Noakes, D.J., McFarlane, G.A., Klyashtorin, L., Ivanov, V.V., Kurashov, V., 1999. The regime concept and natural trends in the production of Pacific salmon. Canadian Journal of Fisheries and Aquatic Science 56, 516-526.

Blood, D.M., This Volume. Low-temperature incubation of walleye pollock (*Theragra chalcogramma*) eggs from the southeastern Bering Sea shelf and Shelikof Strait, Gulf of Alaska. Deep-Sea Research Part II

Bond, N.A., Adams, J.M., (This Volume) Atmospheric forcing of the southeast Bering Sea shelf during 1995-1999 in the context of a 40-year historical record. Deep-Sea Research Part II

Brodeur, R.D., Mills, C.E., Overland, J.E., Walters, G.E., Schumacher, J.D., 1999a Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. Fisheries Oceanography 8, 296-306.

Brodeur, R.D., Sugisaki, H., Hunt, G.L., Jr., In Press. Increases in jellyfish biomass in the Bering Sea: Implications for the ecosystem. Marine Ecology Progress Series.

Brodeur, R.D., Wilson, M.T., Walters, G.E., Melnikov, I.V., 1999b Forage fish in the Bering Sea: distribution, species associations and biomass trends In: Loughlin, T.R., Ohtani, K. (Eds.), Dynamics of the Bering Sea: A Summary of Physical, Chemical, and Biological Characteristics, and a Synopsis of Research on the Bering Sea. University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, Alaska, USA, pp. 509-536.

Brodeur, R.D., Wilson, M.T., Ciannelli, L., 2000. Spatial and temporal variability in feeding and condition of age-0 walleye pollock (*Theragra chalcogramma*) in frontal regions of the Bering Sea. ICES Journal of Marine Science. 57, 256-264.

Brueggerman, J.J., Oliver, G.W., Fowler, C., Frost, K., Fay, K., Cowles, C., Schneider, K., Calkins, D., 1987. Marine Mammals. In: Hameedi, M.J. (Ed.), The St. George Basin environment and possible consequences of planned offshore oil and gas development. U.S. Depart. Commerce, U.S. Dept. Interior, Outer Continental Shelf Environmental Assessment Program, Juneau, Alaska, USA, pp. 55-81.

Bulatov, O.A., 1995. Biomass variations of walleye pollock in the Bering Sea in relation to oceanological conditions. In: Beamish, R.J. (Ed.), Climate change and northern fish populations. Canadian Special Publication in Fisheries and Aquatic Science 121, 631-640.

Ciannelli, L., Brodeur, R., Buckley, T.W., 1998. Development and application of a bioenergetics model for juvenile walleye pollock. Journal of Fish Biology 52, 879-898.

Coachman, L.K., 1986. Circulation, water masses and fluxes on the southeastern Bering Sea shelf. Continental Shelf Research 5, 23-108.

Cooney, R.T., Coyle, K.O., 1982. Trophic implications of cross-shelf copepod distributions in the southeastern Bering Sea. Marine Biology 70, 187-196.

Corkett, C.J., McLaren, I.A., 1978. The biology of *Pseudocalanus*. Advances in Marine Biology 15, 1-231.

Coyle, K.O., Chavtur, V.G., Pinchuk, A.I., 1996. Zooplankton of the Bering Sea: a review of the Russian Literature. In: Mathisen, O.A., Coyle, K.O. (Eds.), Ecology of the Bering Sea: A review of Russian literature. Univ. Alaska Sea Grant Report 96-01, Fairbanks, Alaska, USA, pp. 97-133.

Coyle, K.O., Pinchuk, A.I., This Volume. The abundance and distribution of euphausiids and zero-age pollock on the inner shelf of the southeast Bering Sea relative to the inner front. Deep-Sea Research Part II

Dagg, M.J., Clarke, M.E., Nishiyama, T., Smith, S.L., 1984. Production and standing stock of copepod nauplii, food items for larvae of the walleye pollock *Theragra chalcogramma* in the southeastern Bering Sea. Marine Ecology Progress Series 19, 7-16.

Dagg, M.J., Vidal, J., Whitledge, T.E., Iverson, R.L., Goering, J.J., 1982. The feeding, respiration, and excretion of zooplankton in the Bering Sea during a spring bloom. Deep-Sea Research 29, 45-63.

Decker, M.B., Hunt, G.L., Jr., 1996. Foraging by murres (*Uria* spp.) at the tidal front surrounding the Pribilof Islands, Alaska. Marine Ecology Progress Series 139, 1-10.

Decker, M.B., Hunt, G.L., Jr., Byrd, G.V., Jr., 1995. The relationships among sea surface temperature, the abundance of juvenile walleye pollock (*Theragra chalcogramma*), and the reproductive performance and diets of seabirds at the Pribilof Islands, southeastern Bering Sea. In: Beamish, R.J. (Ed.) Climate change and northern fish populations. Canadian Special Publication in Fisheries and Aquatic Science 121: 425-437.

Dragoo, D.E., Byrd, G.V., Irons, D.B., 2000. Breeding status and population trends of seabirds in Alaska in 1999. U.S. Fish and Wildlife Service Report AMNWR 2000/02.

Dugdale, R.C., Goering, J.J., 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnology and Oceanography 12, 196-206.

Dwyer, D.A., Bailey, K.M., Livingston, P.A., 1987. Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, with special

reference to cannibalism. Canadian Journal of Fisheries and Aquatic Science 44, 1972-1984.

Ebbesmeyer, C.C., Cayan, D.R., Milan, D.R., Nichols, F.H., Peterson, D.H., Redmond, K.T., 1991. 1976 step in the Pacific climate: forty environmental changes between 1968-1975 and 1977-1984. In: Betancourt, J.L., Tharp, V.L. (Eds.), Proceedings of the Seventh Annual Climate (PACLIM) Workshop, April 1990. . California Department of Water Resources, Interagency Ecological Studies Program Technical Report 26, pp. 115-126.

Eslinger. D.L., Iverson, R.L., 2001. The effects of convective and wind-driven mixing on spring phytoplankton dynamics in the southeastern Bering Sea middle shelf domain. Continental Shelf Research 21, 627-650.

Francis, R.C., Hare, S.R., Hollowed, A.B., Wooster, W.S., 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fisheries Oceanography 7, 1-21.

Gervais, F., Riebesell, U., 2001. Effect of phosphorus limitation on elemental composition and stable carbon isotope fractionation in a marine diatom growing under different CO_2 concentrations. Limnology and Oceanography 46, 497-504.

Gifford, D.J., Fessenden, L.M., Garrahan, P.R., Martin, E., 1995. Grazing by microzooplankton and mesozooplankton in the high latitude North Atlantic Ocean: Spring versus summer dynamics. Journal of Geophysical Research 100 (C4), 6665-6675.

Grover, J.J., 1991. Trophic relationship of age-0 and age-1 walleye pollock *Theragra chalcogramma* collected together in the eastern Bering Sea. Fisheries Bulletin 89, 719-722.

Hare, S.R., Francis, R.C., 1995. Climate change and salmon production in the northeast Pacific Ocean. In: Beamish, R.J. (Ed.), Climate change and northern fish populations. Canadian Special Publication in Fisheries and Aquatic Science 121, 357-372.

Hare, S. R., Mantua, N.J., 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47, 103-146.

Hatch, S.A., Byrd, G.V., Jr., Irons, D.B., Hunt, G.L., Jr., 1993. Status and ecology of kittiwakes (*Rissa tridactyla* and *R. brevirostris*) in the North Pacific. In: Vermeer, K, K.T. Briggs, K.H. Morgan, D.C. Siegel-Causey (Eds.), The Status, Ecology and Conservation of Marine Birds of the North Pacific Ocean. Canadian Wildlife Service Special Publication, Ottawa, Canada, pp. 140-153.

Haynes, E.G., Ignell, G., 1983. Effect of temperature on rate of embryonic development of walleye pollock, *Theragra chalcogramma*. Fisheries Bulletin 81, 890-894.

Hillgruber, N., Haldorson, L.J., Paul, A.J., 1995. Feeding selectivity of larval walleye pollock *Theragra chalcogramma* in the oceanic domain of the Bering Sea. Marine Ecology Progress Series 120, 1-10.

Holligan, P.M., Harris, R.P., Newell, R.C., Harbour, D.S., Head, R.N., Linley, E.A.S., Lucas, M.I., Tranter, P.R.G., Weekley, C.M., 1984. Vertical distribution and partitioning of organic carbon in mixed frontal and stratified water of the English Channel. Marine Ecology Progress Series 17, 201-213.

Hollowed, A.B., Hare, S.R., Wooster, W.S., In Press. Pacific-Basin climate variability and patterns of northeast Pacific marine fish production. Progress in Oceanography.

Hunt, G.L., Jr., Byrd, G.V., Jr., 1999. Marine bird populations and carrying capacity of the eastern Bering Sea. In: Loughlin, T.R., Ohtani, K. (Eds.), Dynamics of the Bering Sea. Univ. of Alaska Sea Grant AK-SG-99-03, Fairbanks, Alaska, USA, pp.631-650.

Hunt, G.L., Jr., Baduini, C.L., Brodeur, R.D., Coyle, K.O., Kachel, N.B., Napp, J.M., Salo, S.A., Schumacher, J.D., Stabeno, P.J., Stockwell, D.A., Whitledge, T.E., Zeeman, S.I., 1999. The Bering Sea in 1998: A second consecutive year of extreme weather-forced anomalies. EOS, Transactions of the American Geophysical Union 80, 561, 565-566.

Hunt, G.L., Jr., Baduini, C., Jahncke, J., This Volume. Diets of Short-tailed Shearwaters in the Southeastern Bering Sea. Deep-Sea Research Part II. In Press.

Hunt, G.L., Jr., Coyle, K.O., Hoffman, S., Decker, M.B., Flint, E.N., 1996a. Foraging ecology of short-tailed shearwaters near the Pribilof Islands, Bering Sea. Marine Ecology Progress Series 141, 1-11.

Hunt, G.L., Jr., Decker, M.B., Kitaysky, A.S., 1996b. Fluctuations in the Bering Sea Ecosystem as reflected in the reproductive ecology and diets of kittiwakes on the Pribilof Islands, 1975 to 1990. In: Greenstreet, S., Tasker, M. (Eds.), Aquatic Predators and Their Prey. Blackwell, London, pp. 142-153.

Hunt, G.L., Jr., Kitaysky, A.S., Decker, M.B., Dragoo, D.E., Springer, A.M., 1996c. Changes in the distribution and size of juvenile walleye pollock as indicated by seabird diets at the Pribilof Islands and by bottom trawl surveys in the eastern Bering Sea. In: Brodeur, R.D., Livingston, P.A. Loughlin, T.R., Hollowed, A.B. (Eds.) Ecology of juvenile walleye pollock, *Theragra chalcogramma*. NOAA Technical Report NMFS 126, 133-147.

Huntley, M.E., Lopez, M.D.G., 1992. Temperature-dependent production of marine copepods: a global analysis. American Naturalist 140, 201-242.

Ikeda, T., Motoda, S., 1978. Zooplankton production in the Bering Sea calculated from 1956-1970 Oshoro Maru data. Marine Science Communications 4, 329-346.

Iverson, R.L., Coachman, L.K., Cooney, R.T., English, T.S., Goering, J.J., Hunt, G.L., Jr., Macauley, M.C., McRoy, C.P., Reeburgh, W.S., Whitledge, T.E., 1979a. Ecological significance of fronts in the southeastern Bering Sea. In: Livingston, R.J. (Ed.), Ecological Processes in Coastal and Marine Systems. Plenum Press, New York, pp. 437-466.

Iverson, R.L., Whitledge, T.E., Goering, J.J., 1979b. Chlorophyll and nitrate fine structure in the southeastern Bering Sea shelf break front. Nature 281, 664-666.

Johannessen, O.M., Shalina, E.V., Miles, M.W., 1999. Satellite evidence for an Arctic sea ice cover in transformation. Science 286, 1937-1939.

Kachel, N.B., Hunt, G.L., Jr., Salo, S.A., Schumacher, J.D., Stabeno, P.J., Whitledge, T.E., This Volume Characteristics of the inner front of the southeastern Bering Sea. Deep-Sea Research Part II

Kajimura, H., 1984. Opportunistic feeding of the northern fur seal, *Callorhinus ursinus*, in the eastern North Pacific Ocean and eastern Bering Sea. U.S. Dept. Commerce, NOAA Technical Report NMFS SSRF-779. 49pp.

Khen, G.V., 1987. Interannual changes in water temperatures in the southeastern Bering Sea and its role in oscillation in year class strength of eastern Bering Sea pollock. Populyationnaya struktura, dinamika chislennosti I ekologia mintaya [Population structure, numerical dynamics and ecology of pollock]. Vladivostok, pp. 209-220.

Kinder, T.H., Hunt, G.L., Jr., Schneider, D., Schumacher, J.D., 1983. Correlation between seabirds and oceanic fronts around the Pribilof Islands, Alaska. Estuarine Coastal and Shelf Science 16, 309-319.

Kinder, T.H., Schumacher, J.D., 1981. Hydrographic structure over the continental shelf of the southeastern Bering Sea. In: Hood, D.W., Calder, J.A. (Eds.), The Eastern Bering Sea Shelf: Oceanography and Resources, Vol. 1, US. Government Printing Office, Washington, D.C., pp. 31-52.

Laevastu, T., Bax, N., 1991. Predation-controlled recruitment in the Bering Sea fish ecosystem. ICES Marine Science Symposium 193, 147-152.

Lang, G.M., Brodeur, R.D., Napp, J.M., Schabetsberger, R., 2000. Variation in groundfish predation on juvenile walleye pollock relative to hydrographic structure near the Pribilof Islands, Alaska. ICES Journal of Marine Science. 57, 265-271.

Leatherwood, S., Bowles, A.E., Reeves, R.R., 1983. Aerial surveys of marine mammals in the southeastern Bering Sea. National Oceanic and Atmospheric Administration/Outer Continental Shelf Environmental Assessment Program, Environmental Assessment of the Alaskan Continental Shelf. Final Reports of Principal Investigators 42, 147-473.

Levinson, H., Turner, J.T., Nielsen, T.G., Hansen, B.W., 2000. On the trophic coupling between protests and copepods in arctic marine ecosystems. Marine Ecology Progress Series 204, 65-77.

Libes, S.M., 1992. An introduction to marine biogeochemistry. John Wiley and Son, New York, pp.734.

Livingston, P.A., Jurado-Molina, J., 2000. A multispecies virtual population analysis of the eastern Bering Sea. ICES Journal of Marine Science. 57, 294-299.

Livingston, P.A., Lang, G.M., 1996. Interdecadal comparisons of walleye pollock, *Theragra chalcogramma*, cannibalism in the eastern Bering Sea. In: Brodeur, R.D., Livingston, P.A. Loughlin, T.R., Hollowed, A.B. (Eds.), Ecology of juvenile walleye pollock, *Theragra chalcogramma*. NOAA Technical Report NMFS 126, 115-124.

Livingston, P.A., Low, L-L., Marasco, R.J., 1999. Eastern Bering Sea trends. In Sherman, K., Tang, Q. (Eds.), Large Marine Ecosystems of the Pacific Rim: Assessment, Sustainability, and Management. Blackwell Science, Inc. Malden, Massachusetts, USA, pp. 140-162.

Livingston, P.A., Methot, R., 1998. Incorporation of predation into an assessment model of eastern Bering Sea walleye pollock. In Fishery stock assessment models, Alaska Sea Grant College Program Report No. 98-01, pp.663-678.

Livingston, P.A., Tjelmeland, S., 2000. Fisheries in boreal ecosystems. ICES Journal of Marine Science. 57, 619-627.

Loeng, H., 1989. The influence of temperature on some fish population parameters in the Barents Sea. Journal of Northwest Atlantic Fisheries Science 9, 103-113.

Loughlin, T.R., Antonelis, G.A., Baker, J.D., York, A.E., Fowler, C.W., DeLong, R.L., & Braham, H.W., 1994. Status of the northern fur seal population in the United States during 1992. In: Sinclair, E.H., (Ed.), Fur Seal Investigations, 1994. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-45.

McFarlane, G.A., King, J.R., Beamish, R.J., 2000. Have there been recent changes in climate? Ask the fish. Progress in Oceanography 47, 147-169.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific interdecadal oscillation with impacts on salmon production. Bulletin American Meteorological Society 78, 1069-1079.

McLaren, I.A., 1963. Effects of temperature on growth of zooplankton and the adaptive significance of vertical migration. Journal of the Fisheries Research Board of Canada 20, 685-727.

McRoy, C.P., Mizobata, K., Nakanishi, S., Saito, S-i., 2001. Trends in ocean conditions and new production on the shelf of the southeastern Bering Sea over the past twenty years. PICES Annual Meeting 2001, Victoria, British Columbia. Abstracts.

Merrick, R., 1995. The relationship of the foraging ecology of Steller sea lions (*Eumetopias jubatus*) to their population decline in Alaska. Ph.D. Thesis, Univ. Washington, Seattle, Washington, USA, unpublished.

Merrick, R.L., 1997. Current and historical roles of apex predators in the Bering Sea ecosystem. Journal of Northwest Atlantic Fisheries Science 22, 343-355.

Merrick, R.L., Chumbley, M.K., Byrd, G.V., 1997. A potential relationship between the diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska. Canadian Journal of Fisheries and Aquatic Science 54, 1342-1348.

Methven, D.A., Piatt, J., 1991. Seasonal abundance and vertical distribution of capelin (*Mallotus villosus*) in relation to water temperature at a coastal site off eastern Newfoundland. ICES Journal of Marine Science. 48, 187-193.

Moore, S.E., Waite, J.M., Mazzuca, L.L., Hobbs, R.C., 2000. Mysticete whale abundance and observations of prey associations on the central Bering Sea shelf. Journal of Cetacean Research and Management 2, 227-234.

Müter, F-J, Norcross, B.L., Royer, T.C., 1995. Do cyclic temperatures cause cyclic fisheries? In: Beamish, R.J. (Ed.), Climate change and northern fish populations. Canadian Special Publication in Fisheries and Aquatic Science 121, 119-129.

NMFS (National Marine Fisheries Service), 1993. Final conservation plan for the northern fur seal (*Callorhinus ursinus*). Prepared by the NMFS/Alaska Fisheries Science Center/National Marine Mammal Laboratory, Seattle, Wash. and the NMFS/Office of Protected Resources, Silver Spring, Md. 80pp.

NMFS (National Marine Fisheries Service), 1995. Status review of the United States Steller sea lion (*Eumetopias jubatus*) population. Prepared by the NMFS/Alaska Fisheries Science Center/National Marine Mammal Laboratory, Seattle, Wash. 45 pp.

NRC (National Research Council), 1996. The Bering Sea ecosystem. National Academy Press, Washington, D.C.

Nakatani, T., Maeda, T., 1984. Thermal effect on the development of walleye pollock eggs and on their upward speed to the surface. Bulletin Japan Society Science Fisheries 50, 937-942.

Napp, J. M., Hunt, G. L. Jr., 2001. Anomalous conditions in the southeastern Bering Sea, 1997: Linkages among climate, weather, ocean, and biology. Fisheries Oceanography 10, 61-68.

Napp, J.M., Incze, L.S., Ortner, P.B., Siefert, D.L. W., Britt, L., 1996. The plankton of Shelikof Strait, Alaska: standing stock, production, mesoscale variability and their relevance to larval fish survival. Fisheries Oceanography 5 (Suppl. 1), 19-38.

Napp, J.M., Kendall, A.W., Jr., Schumacher, J.D., 2000. A synthesis of biological and physical processes affecting the feeding environment of larval walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. Fisheries Oceanography 9, 147-162.

Napp, J.M., Baier, C.T., Coyle, K.O., Brodeur, R.D., Shiga, N., Mier, K., This Volume. Interannual and decadal variability in zooplankton communities of the southeastern Bering Sea. Deep-Sea Research Part II.

Naumenko, N.I., 1996. Distribution, biological condition, and abundance of capelin (*Mallotus villosus*) in the Bering Sea. In: Mathisen, O.A., Coyle, K.O. (Eds.), Ecology of the Bering Sea: A review of Russian literature. Univ. Alaska Sea Grant Report 96-01, Fairbanks, Alaska, USA, pp. 237-256.

Niebauer, H.J., Alexander, V., Henrichs, S.M., 1990. Physical and biological oceanographic interaction in the spring bloom at the Bering Sea marginal ice edge zone. Journal of Geophysical Research 95, 22229-22242.

Niebauer, H.J., Alexander, V., Henrichs, S.M., 1995. A time-series study of the spring bloom at the Bering Sea ice edge. I: Physical processes, chlorophyll and nutrient chemistry. Continental Shelf Research 15, 1859-1878.

Niebauer, H.J., Bond, N.A., Yakunin, L.P., Plotnikov, V.V., 1999. An update on the climatology and sea ice of the Bering Sea. In: Loughlin, T.R., Ohtani, K. (Eds.), Dynamics of the Bering Sea: A Summary of Physical, Chemical, and Biological Characteristics, and a Synopsis of Research on the Bering Sea. North Pacific Marine Science Organization (PICES), University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, Alaska, USA, pp. 29-59.

Ohtani, K., Azumaya, T., 1995. Influence of interannual changes in ocean conditions on the abundance of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. In: Beamish, R.J. (Ed.), Climate change and northern fish populations. Canadian Special Publication in Fisheries and Aquatic Science 121: 87-95.

Olson, M.B., Strom, S.L., This Volume. Phytoplankton growth, microzooplankton herbivory and community structure in the southeast Bering Sea: insight into the formation and temporal persistence of an *Emiliania huxleyi* bloom. Deep-Sea Research Part II

Osterkamp, T.E., 1994,   EOS, Transactions of the American Geophysical Union 75, 85.

Overland, J.E., Adams, J.M., Bond, N.A., 1999. Decadal variability of the Aleutian low and its relation to high-latitude circulation. Journal of Climate 12, 1542-1548.

Overland, J.E., Adams, J.M., 2000. On the temporal character and regionality of the Arctic Oscillation. Geophysical Research Letters Accepted

Pahlke, K.A., 1985. Life history and distribution of capelin (*Mallotus villosus*) in Alaskan waters. M.S. Thesis, Univ. Alaska, Juneau, Alaska, USA, Unpublished.

Parker, D.E., Folland, C.K., Ward, M.N., Maskell, K., Bevan, A., Jackson, M., 1993. Ocean-atmosphere climatic fluctuations on interannual to century time scales. Rep. 69, Hadley Centre for Climate Prediction and Research, Bracknell, England, 69 pp.

Pease, C.H., 1980. Eastern Bering Sea ice processes. Monthly Weather Review 108, 2015-2023.

Piatt, J.F., Anderson, P., 1996. Response of common murres to the Exxon Valdez oil spill and long-term changes in the Gulf of Alaska marine ecosystem. American Fisheries Society Symposium 18, 720-737.

Quinn, T.J., Niebauer, H.J., 1995. Relation of eastern Bering Sea walleye pollock (*Theragra chalcogramma*) recruitment to environmental and oceanographic variables. In: Beamish, R.J. (Ed.), Climate change and northern fish populations. Canadian Special Publication in Fisheries and Aquatic Science 121, 497-507.

Ream, R.R., Baker, J.D., Towell, R.G., 1999. Bogoslof Island Studies, 1997. In: Sinclair, E.H., Robson, B.W., (Eds.), Fur Seal Investigations, 1997. U.S. Department of Commerce, NOAA Tech. Memo. NMFS-AFSC-106, 111 pp.

Reid, P.C., Battle, E.J.V., Batten, S.D., Brander, K.M., 2000. Impacts of fisheries on plankton community structure. ICES Journal of Marine Science 57, 495-502.

Rho, T., Goering, J.J., Whitledge, T.E., Stockwell, D.A., This Volume. Carbon and nitrogen uptakes and nutrients response to the warm conditions in the southeastern Bering Sea during 1997 and 1998. Deep-Sea Research Part II.

Richardson, K., Christoffersen, A., 1991. Seasonal distribution and production of phytoplankton in the southern Kattegat. Marine Ecology Progress Series 78, 217-227.

Robson, B.W., 2002. The relationship between foraging areas and breeding sites of lactating northern fur seals, *Callorhinus ursinus* in the eastern Bering Sea. MSc. Thesis, University of Washington, Seattle, WA.

Roff, J.C., Middlebrook, K., Evans, F., 1988. Long-term variations in North Sea zooplankton. Journal of the Marine Biology Association of the U.K. 68, 143-164.

Runge, J.A., 1988. Should we expect a relationship between primary production, fisheries? The role of copepod dynamics as a filter of trophic variability. Hydrobiologia 167/168, 61-71.

Sætersdal, G., Loeng, H., 1987. Ecological adaptation of reproduction in northeast Arctic cod. Fisheries Research 5, 253-270.

Sambroto, R.N., Niebauer, H.J., Goering, J.J., Iverson, R.L., 1986. Relationships among vertical mixing, nitrate uptake and phytoplankton growth during the spring bloom in the southeast Bering Sea middle shelf. Continental Shelf Research 5, 161-198.

Schabetsberger, R., Brodeur, R.D., Ciannelli, L., Napp, J.M., Swartzman, G.L., 2000. Diel vertical migration and interactions of zooplankton and juvenile walleye pollock (*Theragra chalcogramma*) at a frontal region near the Pribilof Islands, Bering Sea. ICES Journal of Marine Science 57, 1283-1295.

Schell, D.M., 2000. Declining carrying capacity in the Bering Sea: Isotopic evidence from whale baleen. Limnology and Oceanography 45, 459-462.

Schumacher, J., Stabeno, P.J., 1998. The continental shelf of the Bering Sea, In: *The Sea*, Vol. XI, The Global Coastal Ocean: Regional Studies, Synthesis, J. Wiley, New York, New York, USA, pp.789-823.

Schumacher, J.D., Bond, N.A., Brodeur, R.D., Livingston, P.A., Napp, J.M., Stabeno, P.J., In Press. Climate change in the southeastern Bering Sea and some consequences for biota. In: Hemple, G., Sherman, K. (Eds.), Large marine ecosystems of the world: trends in exploitation, protection and research.

Schumacher, J.D., Kinder, T.H., Pashinski, D.J., Charnell, R.L., 1979. A structural front over the continental shelf of the eastern Bering Sea. Journal of Physical Oceanography 9, 79-87.

Sinclair, E.H., 1988. Feeding habits of northern fur seals in the eastern Bering Sea. M.S. Thesis, College of Oceanography, Oregon State Univ., Corvallis, Oregon, USA, Unpublished.

Sinclair, E.H., Antonelis, G.A., Robson, B.W., Ream, R.R., Loughlin, T.R., 1996. Northern fur seal, *Callorhinus ursinus*, predation on juvenile walleye pollock, *Theragra*

chalcogramma. In: Brodeur, R.D., Livingston, P.A. Loughlin, T.R., Hollowed, A.B. (Eds.), Ecology of juvenile walleye pollock, *Theragra chalcogramma*. NOAA Technical Report NMFS 126, 167-178.

Sinclair, E., Loughlin, T., Pearcy, W., 1994. Prey selection by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea. Fisheries Bulletin 92, 144-156.

Smith, S.L., Vidal, J., 1984. Spatial and temporal effects of salinity, temperature, and chlorophyll on the communities of zooplankton in the southeastern Bering Sea. Journal of Marine Research 42, 221-25784:

Smith, S.L., Vidal, J., 1986. Variations in the distribution, abundance and development of copepods in the southeast Bering Sea in 1980 and 1981. Continental Shelf Research 5, 215-239.

Spencer, P.D., Collie, J.S., 1996. A simple predator-prey model of exploited marine fish populations incorporating alternative prey. ICES Journal of Marine Science 53, 615-628.

Springer, A.M., 1992. A review: Walleye pollock in the North Pacific- how much difference do they really make? Fisheries Oceanography 1, 80-96.

Springer, A.M., 1996. Prerecruit walleye pollock, *Theragra chalcogramma*, in seabird food webs of the Bering Sea. In: Brodeur, R.D., Livingston, P.A. Loughlin, T.R., Hollowed, A.B. (Eds.), Ecology of juvenile walleye pollock, *Theragra chalcogramma*. NOAA Technical Report NMFS 126, 198-201.

Springer, A.M., 1998. Is it all climate change? Why marine bird and mammal populations fluctuate in the North Pacific. In: Holloway, G., Muller, P., Henderson, D. (Eds.), Proceedings of the 10th 'Aha Huliko'a Hawaiian Winter Workshop on Biotic

Impacts of Extratropical Climate Variability in the Pacific, January 26-30, 1998. SOEST Special Publication, pp.121-125.

Springer, A.M., McRoy, C.P., Flint, M.V., 1996a. The Bering Sea green belt: shelf-edge processes and ecosystem production. Fisheries Oceanography 5, 205-223.

Springer, A.M., Piatt, J.F., Van Vliet, G.B., 1996b. Seabirds as proxies of marine habitats and food webs in the western Aleutian arc. Fisheries Oceanography 5, 45-55.

Stabeno, P.J., Kachel, N.B., Sullivan, M., Whitledge, T.E., This Volume. Variability along the 70 m isobath of the southeastern Bering Sea. Deep Sea Research Part II

Stabeno, P.J., Schumacher, J.D., Davis, R.F., Napp, J.M., 1998. Under-ice observations of water column temperature, salinity, and spring phytoplankton dynamics: Eastern Bering Sea shelf. Journal of Marine Research 56, 239-255.

Stabeno, P.J., Schumacher, J.D., Ohtani, K., 1999. The physical oceanography of the Bering Sea. In: Loughlin, T.R., Ohtani, K. (Eds.), Dynamics of the Bering Sea: A Summary of Physical, Chemical, and Biological Characteristics, and a Synopsis of Research on the Bering Sea, T.R. Loughlin and K. Ohtani (eds.), North Pacific Marine Science Organization (PICES), University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, Alaska, USA, pp. 1–28.

Stabeno, P.J., Bond, N.A., Kachel, N.B., Salo, S.A., Schumacher, J.D., 2001. On the temporal variability of the physical environment over the southeastern Bering Sea. Fisheries Oceanography 10, 81-98.

Steele, J.H., Henderson, E.W., 1984. Modeling long-term fluctuations in fish stocks. Science 224, 985-987.

Stockwell, D. A., Whitledge, T.E., Zeeman, S.I., Coyle, K.O., Napp, J.M., Brodeur, R.D., Pinchuk, A.I., Hunt, G.L., Jr. 2001. Anomalous conditions in the south-eastern Bering Sea, 1997: Nutrients, phytoplankton, and zooplankton. Fisheries Oceanography 10, 99-116.

Sugimoto, T., Tadokoro, K., 1997. Interannual-interdecadal variations in zooplankton biomass, chlorophyll concentration and physical environment in the subarctic Pacific and Bering Sea. Fisheries Oceanography 6, 74-93.

Sugimoto, T., Tadokoro, K., 1998. Interdecadal variations of plankton biomass and physical environment in the North Pacific. Fisheries Oceanography 7, 289-299.

Swartzman, G., Napp, J.M., Brodeur, R.D., Winter, A., Ciannelli, L., This Volume. Spatial aspects of pollock and zooplankton distribution in the Pribilof Island pollock nursery area. Deep-Sea Res. Part II

Tomasada, A., Odate, K., 1995. Long-term variability in zooplankton biomass and environment. *Umi to Sora* 71, 1-7. (in Japanese)

Tortell, P.D., Rau, G.H., Morel, F.M.M., 2000. Inorganic carbon acquisition in coastal Pacific phytoplankton communities. Limnology and Oceanography 45, 1485-1500.

Townsend, D.W., Cammen, L.M., Holligan, P.M., Campbell, D.E., Pettigrew, N.R., 1994. Causes and consequences of variability in the timing of spring phytoplankton blooms. Deep-Sea Research 41, 747-765.

Trenberth, K.E., Hurrell, J.W., 1995. Decadal coupled atmospheric-ocean variations in the North Pacific Ocean. In: Beamish, R.J. (Ed.), Climate change and northern fish populations. Canadian Special Publication in Fisheries and Aquatic Science 121, 15-24.

Trites A. W., Livingston P. A., Vasconcellos M. C., Mackinson S., Springer A. M., Pauly D., 1999. Ecosystem change and the decline of marine mammals in the Eastern Bering Sea: testing the ecosystem shift and commercial whaling hypotheses. Fisheries Centre Reports 7 (1), 98 pp.

Van Pelt, T.I., Piatt, J.F., Lance, B.K., & Roby, J.F. 1997. Proximate composition and energy density of some North Pacific forage fish. Comparative Biochemistry and Physiology 118A, 1393-1398.

Vance, T.C., Baier, C.T., Brodeur, R.D., Coyle, K.O., M. B. Decker, M.B., Hunt , G.L., Jr., Napp, J.M., Schumacher, J.D., Stabeno, P.J., Stockwell, D., Tenant, C.T., Whitledge, T.E., Wyllie-Echeverria, T., Zeeman, S., 1998. Anomalies in the Ecosystem of the Eastern Bering Sea: Including Blooms, Birds and Other Biota. EOS, Transactions of the American Geophysical Union 79 (10), 121/126.

Vidal, J., 1980. Physioecology of zooplankton II: Effects of phytoplankton concentration, temperature, and body size on the development and molting rates of *Calanus pacificus* and *Pseudocalanus* spp. Marine Biology 56, 135-146.

Vidal, H., Smith, S.L., 1986. Biomass, growth and development of population of herbivorous zooplankton in the southeastern Bering Sea. Deep-Sea Research 33, 523-566.

Vinnikov, A.V., 1996. Pacific cod (*Gadus macrocephalus*) of the western Bering Sea. In: Mathisen, O.A., Coyle, K.O. (Eds.), Ecology of the Bering Sea: A review of Russian literature. Univ. Alaska Sea Grant Report 96-01, Fairbanks, Alaska, USA, pp. 183-202.

Wadhams, P., 2000. Further evidence of ice thinning in the Arctic Ocean. Geophysical Research letters 27 (24), 3973-3975.

Walsh, J.J., McRoy, C.P., 1986. Ecosystem analysis in the southeastern Bering Sea. Continental Shelf Research 5, 259-288.

Wespestad, V.G., 1991. Pacific herring population dynamics, early life history and recruitment variation relative to eastern Bering Sea oceanographic factors. Ph.D. Thesis, Univ. of Washington, Seattle, Washington, USA, Unpublished.

Wespestad, V.G., 1994. Walleye Pollock. Report and data submitted for the Third International Pollock Assessment Workshop. Seattle, WA. Pp. 119-143.

Wespestad, V.G., Quinn, T.J., II., 1996. Importance of cannibalism in the population dynamics of walleye pollock, *Theragra chalcogramma*. In: Brodeur, R.D., Livingston, P.A. Loughlin, T.R., Hollowed, A.B. (Eds.), Ecology of juvenile walleye pollock, *Theragra chalcogramma*. NOAA Technical Report NMFS 126, 212-216.

Wespestad, V.G., Fritz, L.W., Ingraham, W.J., Megrey, B.A., 2000. On relationships between cannibalism, climate variability, physical transport, and recruitment success of Bering sea walleye pollock (*Theragra chalcogramma*). ICES Journal of Marine Science. 57, 272-278.

Whitledge, T.E., 1999. Nutrient cycling and phytoplankton growth. In: Macklin, S.A. (Ed.), Report on the FOCI International Workshop on Recent Conditions in the Bering Sea, Pacific Marine Environmental Laboratory, Seattle, pp. 13-14.

Whitledge, T.E., Reeburgh, W.S., Walsh, J.J., 1986. Seasonal inorganic nitrogen distribution and dynamics in the southeastern Bering Sea. Continental Shelf Research 5, 109-132.

Witherell, D., Pautzke, C., Fluharty, D., 2000. An ecosystem-based approach for Alaska groundfish fisheries. ICES Journal of Marine Science. 57, 771-777.

Withrow, D.E., Loughlin, T.R., 1995. Abundance and distribution of harbor seals (*Phoca vitulina richardsi*) along the north side of the Alaska Peninsula and Bristol Bay during 1995. In: Marine Mammal Protection Act and Endangered Species Act Implementation Program, 1995. National Marine Mammal Laboratory, National Marine Fisheries Service/NOAA, Seattle WA, November 1996.

Wyllie-Echeverria, T., 1995. Sea-ice conditions and the distribution of walleye pollock (*Theragra chalcogramma*) on the Bering and Chukchi shelf. In: Beamish, R.J. (Ed.), Climate change and northern fish populations. Canadian Special Publication in Fisheries and Aquatic Science 121: 131-136.

Wyllie-Echeverria, T., 1996. The relationship between the distribution of one-year-old walleye pollock, *Theragra chalcogramma*, and sea-ice characteristics In: Brodeur, R.D., Livingston, P.A. Loughlin, T.R., Hollowed, A.B. (Eds.), Ecology of juvenile walleye pollock, *Theragra chalcogramma*. NOAA Technical Report NMFS 126, 47-56.

York, A.E., Hartley, J.R., 1981. Pup production following harvest of female northern fur seals. Canadian Journal of Fisheries and Aquatic Science 38, 84-90.

York, A.E., Kozloff, P., 1986. On estimating the number of fur seal pups born on St. Paul Island 1980-1986. Fishery bulletin 85, 367-375.

York, A.E., Towell, R.G., Ream, R.R., Baker, J.D., Robson, B.W., 2000. Population assessment, Pribilof Islands, Alaska. In: Robson, B.W. (Ed.) Fur Seal Investigations, 1998. U.S. Department Commerce, NOAA Technical Memorandum NMFS-AFSC-113, pp. 7-26.

Zeeman, S.I., 1992. The Importance of Primary Production and CO_2. In: Nagel, P.A. (Ed.), Results of the Third Joint US-USSR Bering and Chukchi Seas Expedition (BERPAC), Summer 1989. US Fish and Wildlife Service, Washington, D.C., USA, pp. 218-224.

Figure Legends

Figure 1: The southeastern Bering Sea shelf, with the strata into which the data from the National Marine Fisheries Service bottom trawl surveys were binned. The coastal domain is inshore of the 50 m isobath, the middle domain is between the 50 and 100 m isobaths and the outer domain is between the 100 and 200 m isobaths.

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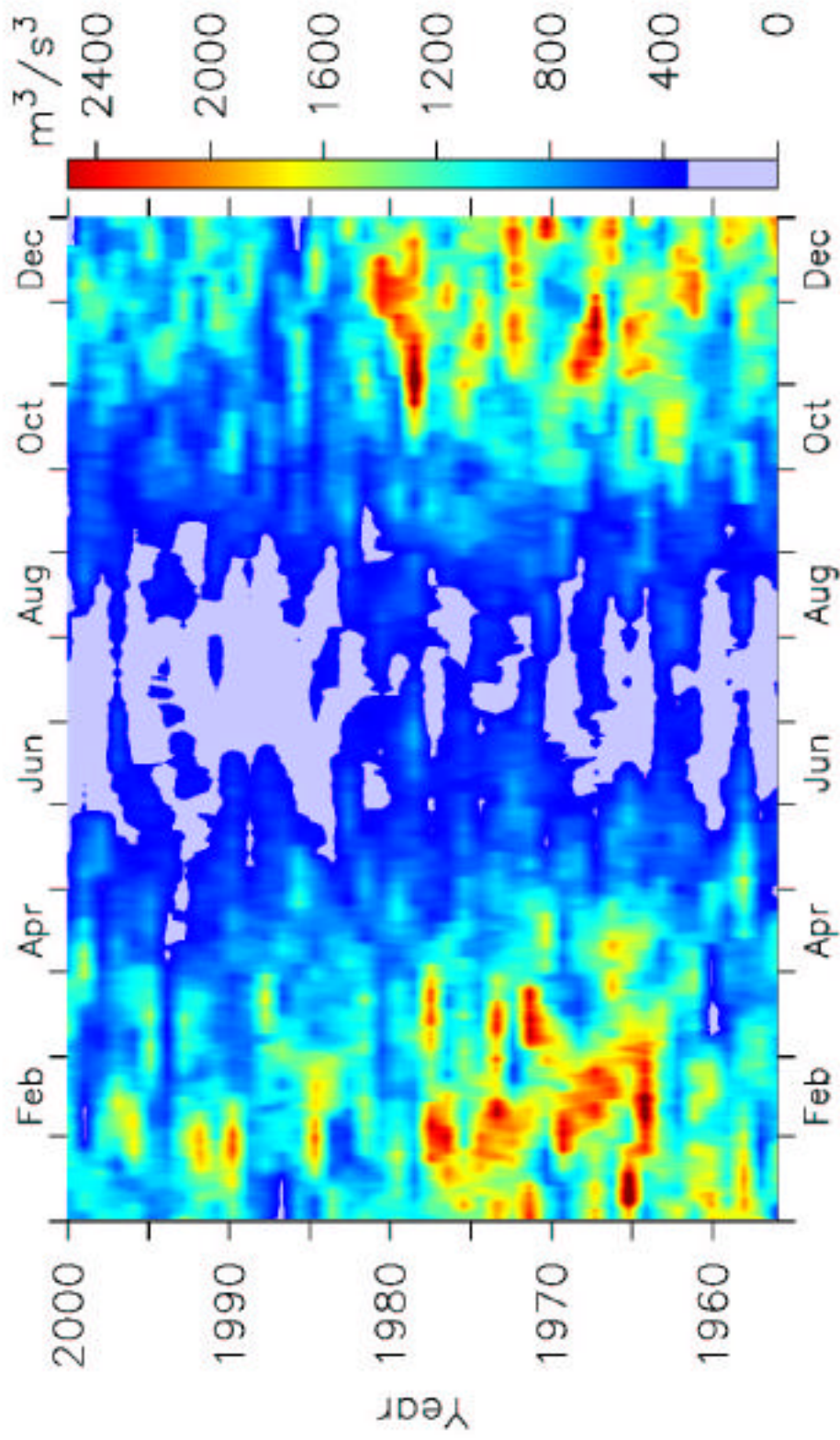
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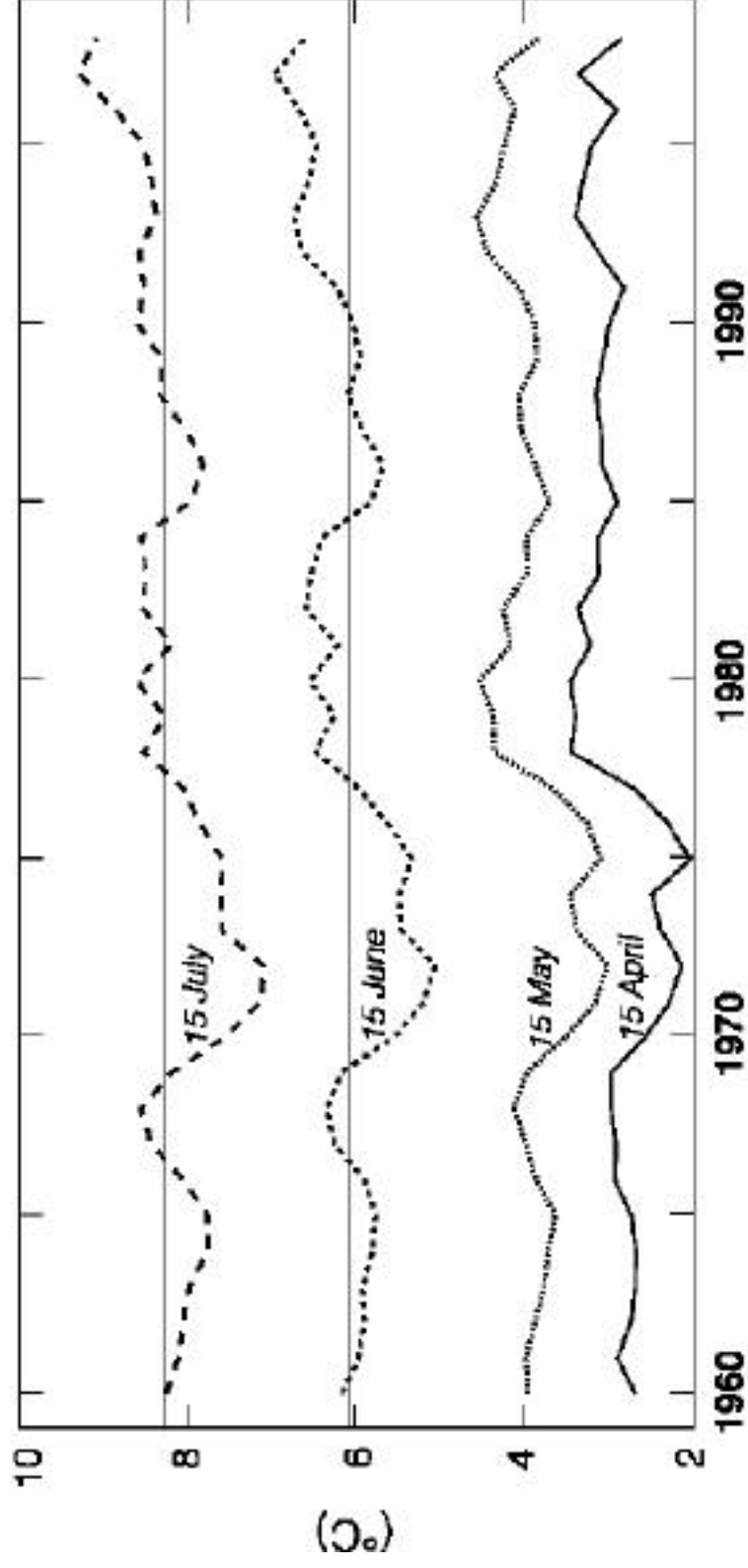
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Figure 6: Time series of temperature profiles at a mooring (M2) in the middle domain. Areas of black indicate cold water resulting from the presence of melting sea ice. The yellow line near the bottom of each panel indicates fluorescence at 11 -13 m. For each year, fluorometer traces have been scaled to the highest value in that year. Gaps in the fluorometer record are the result of fouling of the instrument. Note that when ice is present in or after late March, a strong fluorescence peak occurs as the ice retreats (1995, 1997). When there is no ice (1996) or the ice retreats before late March (1998, 2000), an open-water bloom occurs in May or June. In 1999, the spring was stormy and ice recurred in May. There was a bloom in late March, and another weak and prolonged period of production in late May and June.

Figure 7: Timing of the last retreat of significant ice cover, the timing of the shift from winter wind conditions to summer winds, and their effect on the timing of the spring bloom in the central portion of the middle domain. Note that ice-related or early blooms (to the right of the dotted line) occur in years when the ice retreat comes in late March or later. Early ice retreats lead to May or June blooms (to the left of the doted line). In 1975, there was an ice-related bloom in May. The date of the last winter storm was defined as when the wind speed cubed fell below 2500 m^3 s^{-3} for the summer. The winds were measured at St. Paul Island. Data on the date of the bloom : 1975-1978, Alexander and Cooney, 1979; 1979, 1980, 1981, from Sambroto et al., 1986; 1995-2000, Mooring 2, this study.

Figure 8: Schematic illustration of the relationship between the timing of the retreat of sea ice in the spring, and the timing of the spring bloom. Top: When the ice retreats in late winter, there is insufficient light to support a bloom, and the bloom is delayed until late spring when solar heating has stratified the water column sufficiently to prevent algal cells from sinking. Bottom: When the ice retreat comes later in the spring, then there is sufficient light to support an ice-associated bloom. This bloom can start under the ice, or at the ice edge in ice-melt-stabilized water.

Figure 9: Changes in zooplankton biomass at stations in regions of the deep basin of the Bering Sea and in the outer, middle and coastal domains of the southeastern Bering Sea shelf sampled during the Oshoro Maru Summer Cruises. Data from 1977 to 1994 from Sugimoto and Tadakoro (1998). Data from 1995 to 1999 from Dr. N. Shiga, unpublished. Means with standard errors.

Figure 10: Comparison of the trends in catch per unit effort for jellyfish and the three-year running mean for forage fish, by stratum in the southeastern Bering Sea. See Figure 1 for location of strata. To show trends, the scales of the y-axes vary between strata.

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          B: Changes in the catch per unit effort of flatfish, including rock sole, yellowfin sole (   ) and arrowtooth flounder in the NMFS bottom trawl surveys. Area covered includes all strata. Smoothed line is a 3-year running mean.
          C: Changes in the catch per unit effort of forage fish, including age-1 pollock, age-1 Pacific cod, Pacific herring, eulachon, and capelin in the NMFS bottom trawl surveys. Area covered includes all strata. Smoothed line is a 3-year running mean.

Figure 12: Comparison of the trends in catch per unit effort for age-1 pollock and age-2+ pollock in the NMFS bottom trawl surveys, by stratum in the southeastern Bering Sea. See Figure 1 for location of strata. To show trends, the scales of the y-axes vary between strata.

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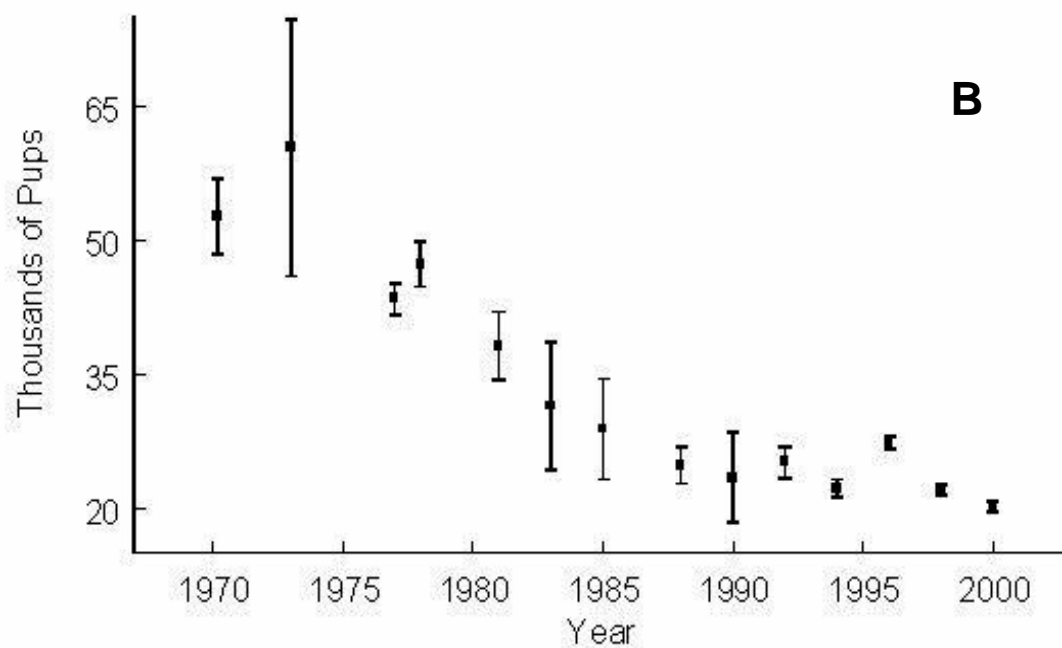
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Figure 15: Harbor seal numbers at haulouts on the north side of the Alaska Peninsula. (Withrow and Loughlin, 1995).

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Figure 18: Schematic illustration of the function of the Oscillating Control Hypothesis. The number of recruits affects not only pollock population dynamics, but also the availability of age-1 pollock to predators such as marine birds and pinnipeds.
Top Panel: In a cold regime, copepod production is limited by water temperature and larval/juvenile pollock survival is limited by food availability.
Upper Middle Panel: At the beginning of a warm regime, copepods flourish and provide ample food resources to support strong survival of larval and juvenile pollock; juvenile pollock survival is high because there are few large piscivorous fish to predate them.
Lower Middle Panel: In a warm regime, the production of copepod food for larval and juvenile pollock remains strong, but survival of juveniles and recruitment is limited by cannibalism from the growing biomass of adult pollock and other predators such as Pacific cod and arrowtooth flounder.
Bottom Panel: At the beginning of a cold regime, copepod production is limited and larval and juvenile pollock are food limited. In addition, cannibalism by adult pollock and other predators further limit recruitment. Thus, there are asymmetries in how pollock recruitment will respond to changes from a cold to a warm regime vs. from a warm to a cold regime.
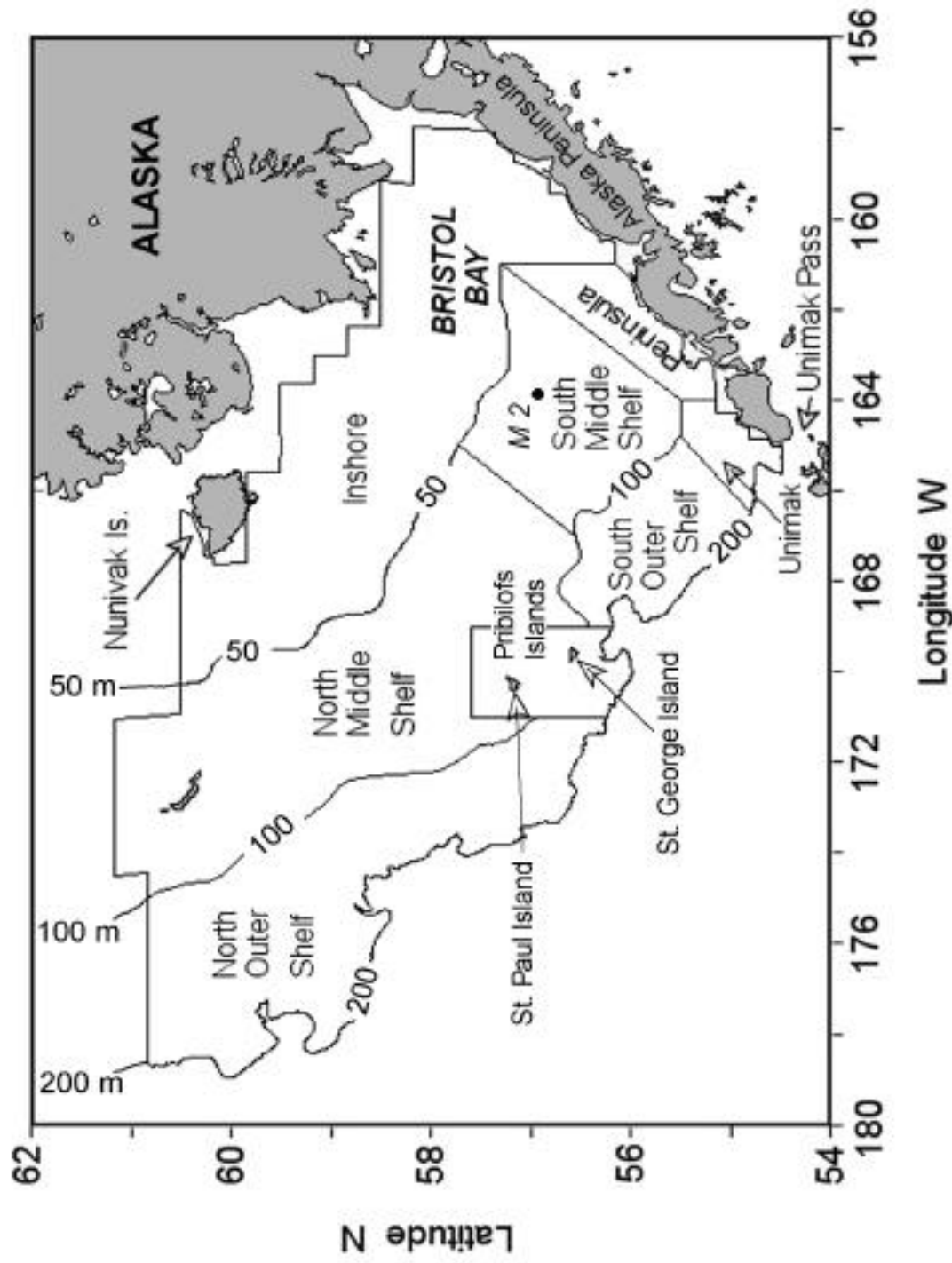
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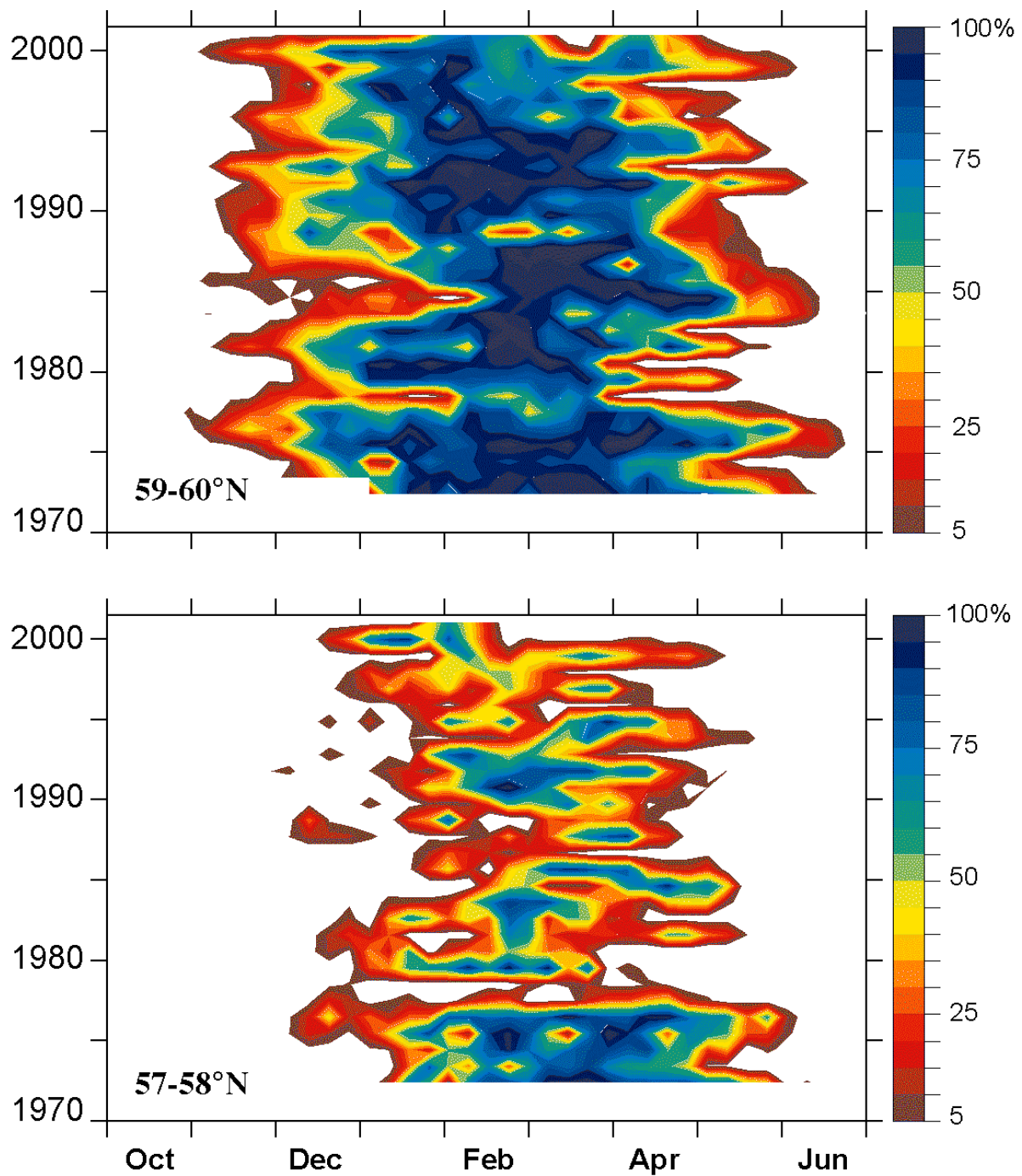
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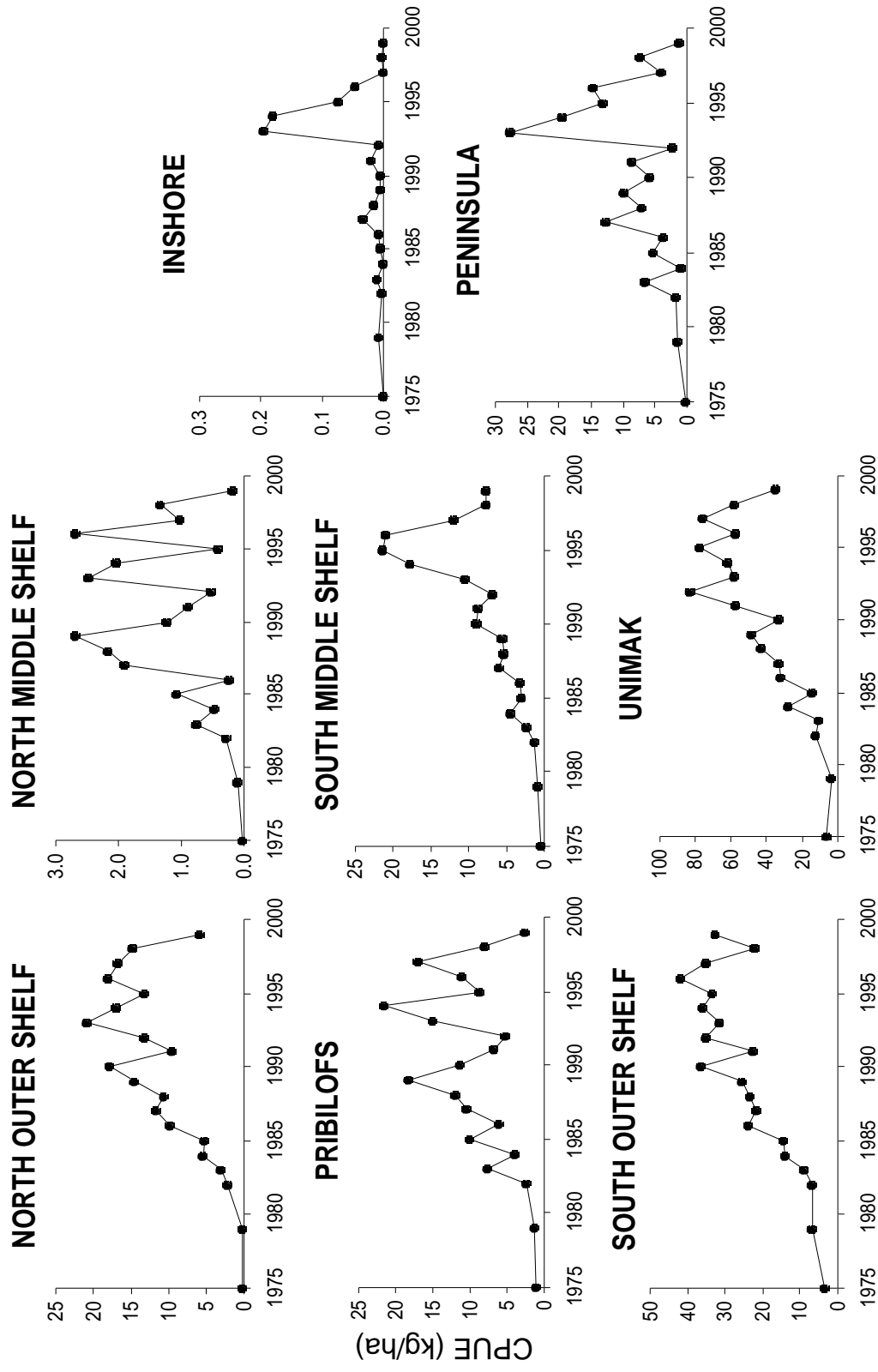
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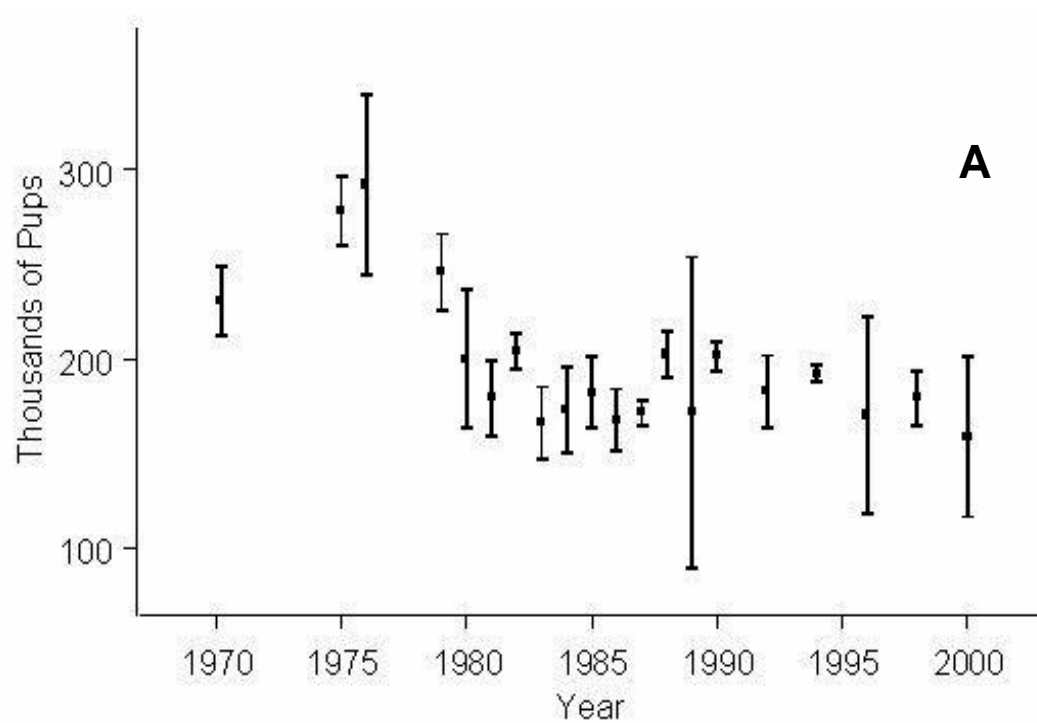
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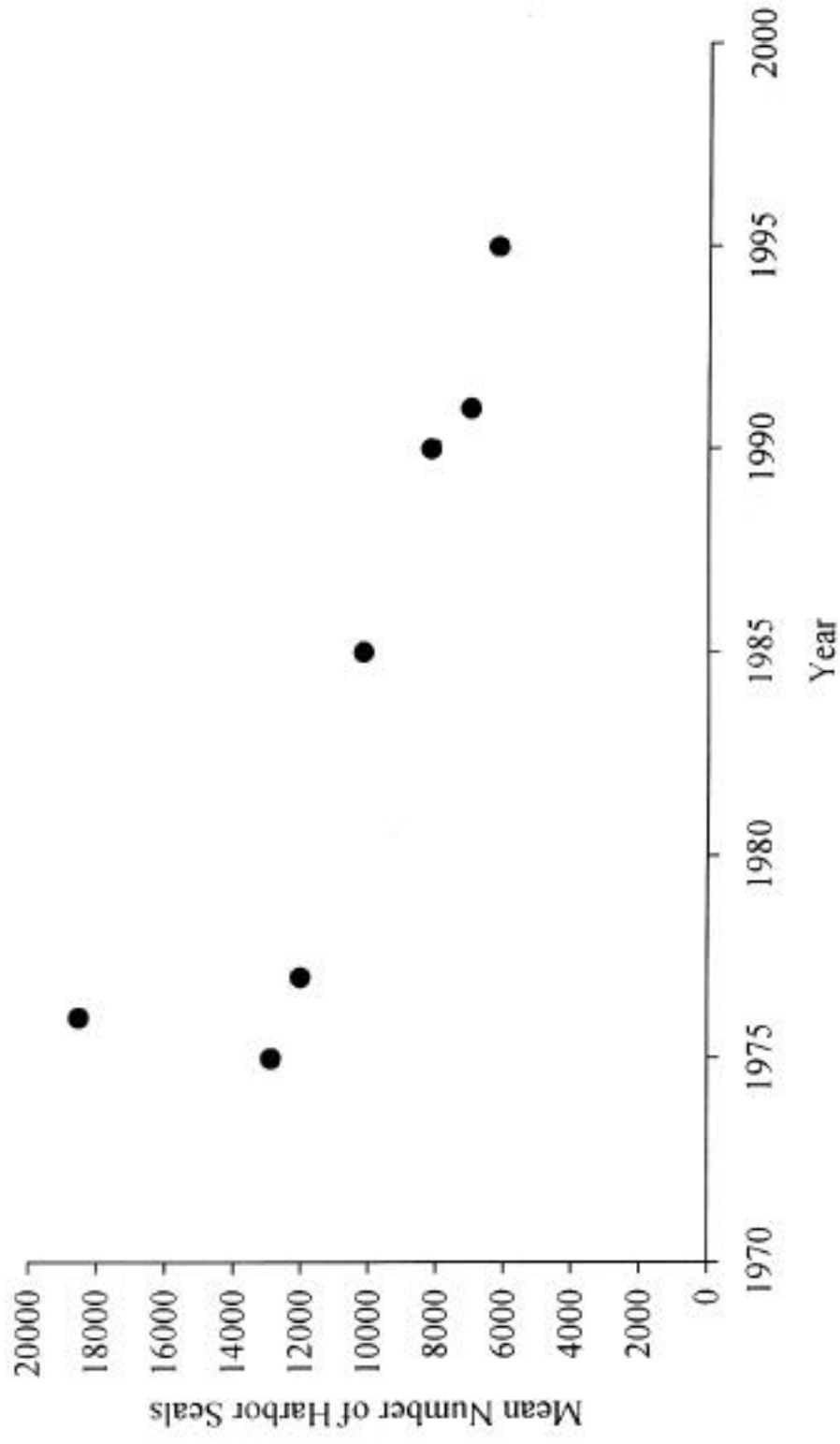
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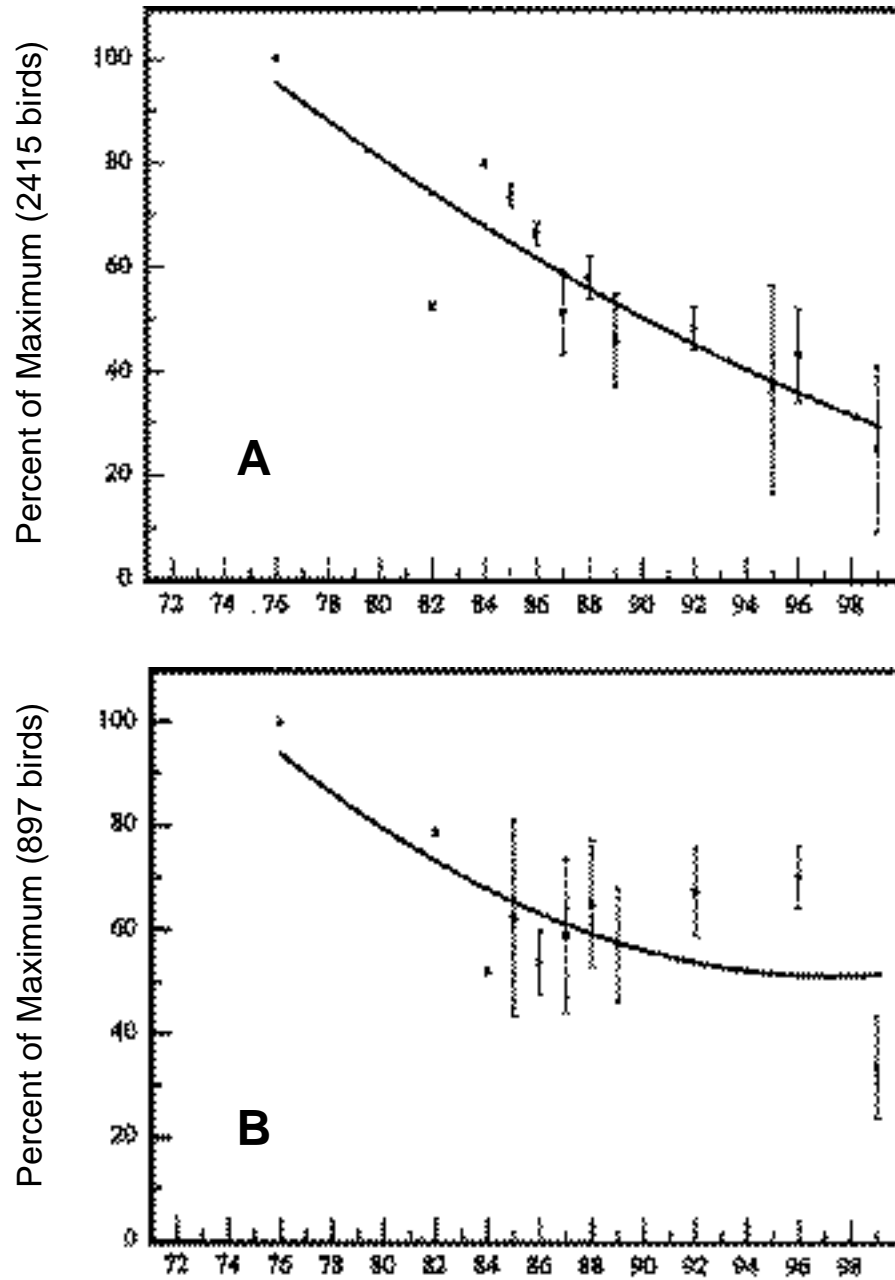
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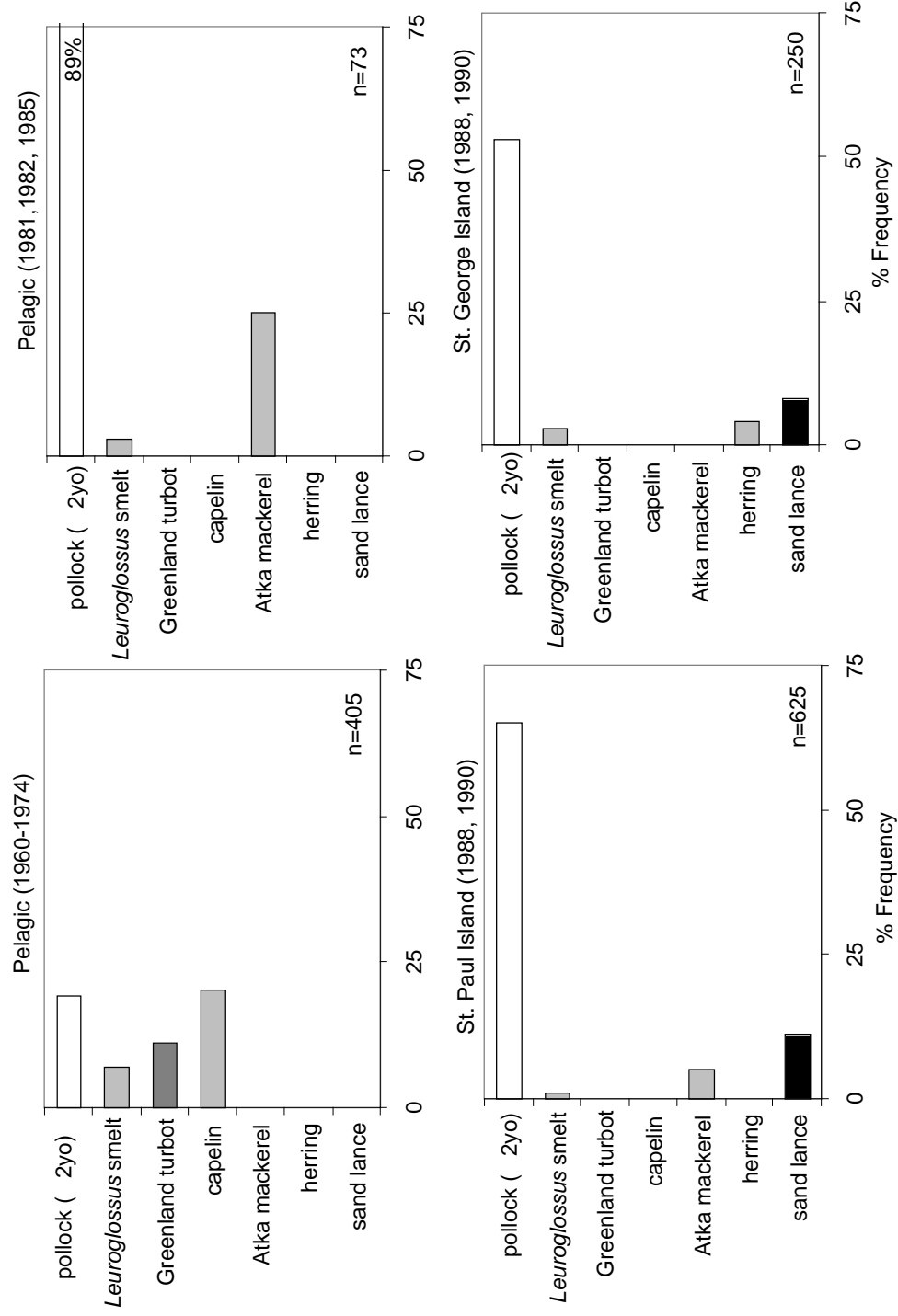
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Oscillating Control Hypothesis

Cold Regime

(Bottom-Up Regulation)

Beginning of Warm Regime

(Bottom-Up Regulation)

Warm Regime

(Top-Down Regulation)

Beginning of Cold Regime

(Both Top-Down and Bottom-Up Regulation)

Zooplankton   Larval Survival   Abundance of Piscivorous Adult Fish   Juvenile Recruits
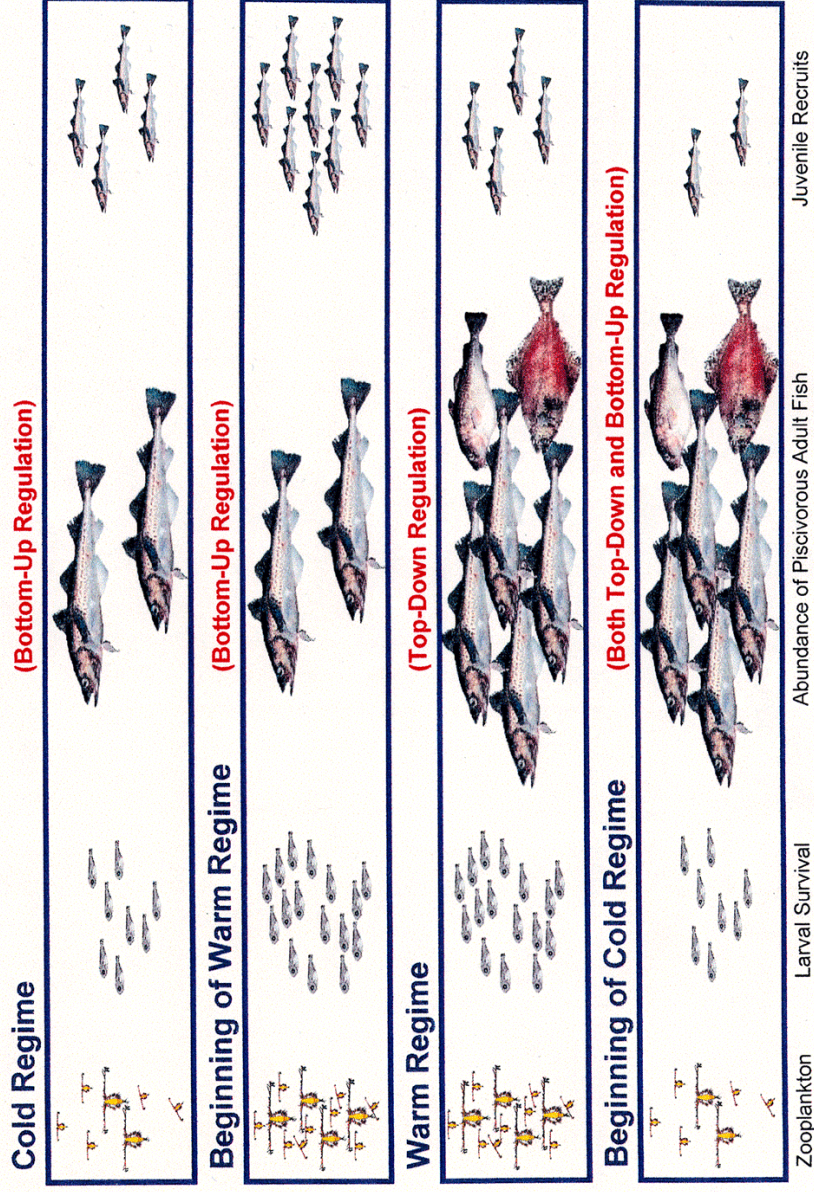
Figure 18: Schematic illustration of the function of the Oscillating Control Hypothesis. The number of recruits affects not only pollock population dynamics, but also the availability of age-1 pollock to predators such as marine birds and pinnipeds. *Top Panel:* In a cold regime, copepod production is limited by water temperature and larval/juvenile pollock survival is limited by food availability. *Upper Middle Panel:* At the beginning of a warm regime, copepods flourish and provide ample food resources to support strong survival of larval and juvenile pollock; juvenile pollock survival is high because there are few large piscivorous fish to predate them. *Lower Middle Panel:* In a warm regime, the production of copepod food for larval and juvenile pollock remains strong, but survival of juveniles and recruitment is limited by cannibalism from the growing biomass of adult pollock and other predators such as Pacific cod and arrowtooth flounder. *Bottom Panel:* At the beginning of a cold regime, copepod production is limited and larval and juvenile pollock are food limited. In addition, cannibalism by adult pollock and other predators further limit recruitment. Thus, there are asymmetries in how pollock recruitment will respond to changes from a cold to a warm regime vs. from a warm to a cold regime.